DRIVERS OF PLANT AND ARTHROPOD DIVERSITY AND COMMUNITY STRUCTURE IN A GRASSLAND ECOSYSTEM

By

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THESIS ABSTRACT

Forces operating at different spatial scales are known to influence species coexistence and community organization, although the relative importance of these forces is debated. While niche-based models emphasize the effect of local processes on community structure, regional species pools and dispersal abilities of organisms are also thought to constrain species distributions and community diversity. To discern the roles of local and regional processes in shaping ecological communities, this thesis examines the importance of factors operating at multiple spatial scales in governing plant diversity and arthropod community structure.

Plant diversity is generally hypothesized to be limited by local competition/productivity ("niche limitation hypothesis", "NLH"), and/or by regional species pools/dispersal ("species pool hypothesis", "SPH"); however, these factors likely interact and vary over periods of community development, *i.e.* succession. For my first chapter, I test the relevance of the SPH and NLH in limiting diversity, in addition to testing how the importance of these factors may shift from seed/dispersal constraints to local competition/productivity over gradients of 1) productivity and 2) time. Species availability and soil nutrient (N and P) availability were manipulated via seed and fertilizer additions, respectively, and diversity responses were measured over the first 11 years of succession. Diversity increased with seed addition and increased species availability, in support of the SPH; and decreased with nutrient addition and the amplification of local competition, in support of the NLH. Species availability became less important in determining species richness as local productivity and pressures of competition increased. Also, positive effects of seed addition dampened with time, suggesting that species/dispersal constraints became less important and local competition/microsite availability became more important over succession. Additionally, species availability mediated effects of soil resources/competition over

time. These results suggest that limits to diversity act at both local and regional scales, and shift in their degree of influence over gradients of successional time and habitat productivity.

The diversity of basal resources is generally predicted to determine diversity at higher trophic levels, as are additional characteristics of local resources (*e.g.* abundance) and regional spatial processes (*e.g.* dispersal, species availability). Yet, the relative importance of these processes is unclear. For my second chapter, I test the importance of basal resources (*i.e.* plants) and spatial processes on community structure of higher trophic levels (*i.e.* consumers). I examine arthropod responses to management/prairie restoration regimes in old-field plant communities, and predict that more diverse and abundant arthropod communities will result from 1) increased resource diversity ("resource diversity hypothesis"), 2) increased resource availability ("resource abundance hypothesis"), and/or 3) increased plant litter density ("plant litter hypothesis"). Additionally, I test arthropod community responses to plant species composition, spatial processes, and direct effects of treatments; and examine responses at the whole community level and within nested microhabitats. I found support for both the resource diversity hypothesis and plant litter hypothesis, and detected effects of plant species composition and spatial processes on community structure. Assemblages occupying distinct microhabitats (and presumably different niche space) varied in their responses to these factors, suggesting that niche-specific processes influence community organization. These results suggest that both characteristics of local resources and regional spatial processes significantly influence consumer community structure; however, as considerable variation is left unexplained, other unaccounted factors are likely to be important in structuring consumer communities.

Overall, this thesis demonstrates that community development and organization of ecological communities are influenced both by regional processes of dispersal and species

availability and by local processes of competition and resource gradients. These processes interact and vary over time and space, highlighting the importance of spatial and temporal scales in understanding determinants of community structure.

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GENERAL INTRODUCTION:

The determinants of species distributions and biodiversity – stemming from questions first raised by Darwin and Wallace (et al) in the 19th century – have been the basis for much of ecology's longest standing questions and prevailing interests (May, 1988). Several conspicuous patterns of diversity have consistently attracted attention, such as latitudinal and altitudinal gradients, species-area curves, and relationships between diversity and productivity (Huston, 1994; Rosenzweig, 1995). Processes creating these patterns and, more generally, driving the formation of ecological communities have often been viewed as occurring at two broad spatial and temporal scales: regional/historical processes and local/deterministic processes (Ricklefs, 1987). Historic events of speciation, extinction, and environmental change are considered to influence species distributions at relatively large geographic scales over long periods of time (Ricklefs, 1987); whereas deterministic processes of competition (Gause, 1934a, 1934b; Huston, 1979) and niche partitioning (Hutchinson, 1959; Macarthur, 1958) are considered to occur at fine (local) geographic scales and over relatively short time periods. Yet, these scales can vary greatly depending on the ecological system of interest (Huston, 1999).

Regional species pools, *i.e.* sets of species capable of colonizing and coexisting in certain areas (Eriksson, 1993; Zobel, 1997), form from events of speciation and extinction and are influenced by the evolutionary history of habitats (Zobel et al., 2011). Regional species pools are hypothesized to determine local diversity, such that patterns observed at the local scale are expected to represent a sample from the regional pool (*i.e.* proportional sampling: Cornell & Lawton, 1992; Zobel, 1997). Positive linear relationships between the size of regional species pool and observed local richness have been found in support of this hypothesis (Caley & Schluter, 1997; Cornell, 1985a, 1985b; Partel et al., 1996). In addition to pool size, other

characteristics of species pools – such as species availability and dispersal – can limit diversity and influence species composition. Accordingly, past demonstrations of species availability and dispersal limitation have found communities to be unsaturated with species and open to additional colonization (Clark et al., 2007; Foster & Tilman, 2003; Turnbull, Crawley, & Rees, 2000).

At relatively smaller spatial scales, local niche-based processes are hypothesized to limit species coexistence in a community through abiotic (environmental conditions) and biotic (competition and predation) filtering (*e.g.* Grime, 1979; Huston, 1999; Davis et al., 2000). Abiotic filters of habitat and resource heterogeneity may determine the number of unique niches available to species, with increasing levels of heterogeneity expected to promote niche partitioning and species coexistence (Harpole & Tilman, 2007; Schoener, 1974).

Habitat productivity is thought to be another filter that influences the strength of local competition, such that increasingly productive sites are predicted to experience higher rates of competitive exclusion, thus reducing the capacity for species coexistence (Huston, 1994, 1999; Tilman, 1993). At local scales, diversity is predicted to share a unimodal relationship with diversity, such that diversity is highest at intermediate levels of productivity (Huston, 1994; Mittelbach et al., 2001; Rosenzweig, 1995); therefore, negative effects of productivity on diversity may correspond to the high productivity (descending) portion of the diversity-productivity curve. However, diversity may be maintained under conditions of high productivity if periodic disturbances reduce the vigor of dominant species and rates of competitive exclusion among subordinates (Foster et al., 2009; Laliberte et al., 2013), as predicted by the Dynamic Equilibrium Model ("DEM": Huston, 1979, 1994).

While the role of productivity in limiting species coexistence and diversity – and its contingency on local disturbance intensity – has been recognized as being influential in community organization, productivity and local competition may mediate the effects of regional species pools on diversity, or vice versa. The "productivity shifting limitations hypothesis" ("SLH_{Prod}") predicts increased productivity to dampen positive effects of large species pools and high species availability on diversity by increasing the importance of local competition and rates of competitive exclusion (Dickson & Foster, 2008; Foster et al., 2004; Houseman & Gross, 2006; Huston, 1999; Partel et al., 2000). On the other hand, species availability has been seen to mediate the expression of species sorting and diversity along resource and productivity gradients (Foster & Dickson, 2004; Foster et al., 2011), demonstrating the reciprocity of interactions between regional and local processes.

In this thesis, I examine responses of communities to processes acting at both local (*e.g.* plant productivity, soil fertility, resource diversity) and regional (*e.g.* dispersal, species availability) scales among plants and arthropods. Generally, plant diversity is hypothesized to be limited by local competition and productivity ("niche limitation hypothesis", "NLH") and/or regional species pools and dispersal ("species pool hypothesis", "SPH"); yet, these factors may interact or shift in relative importance over space and time. As previously mentioned, factors most relevant in limiting diversity may shift from species availability and dispersal constraints to local competition and resource availability along a gradient of increasing productivity, as predicted by the SLH_{Prod} (Foster et al., 2004; Huston, 1999). Additionally, the influence of species constraints and local competition on diversity may vary over the course of community development. During secondary succession, the abundance of microsites and available resources is expected to decline as colonists – particularly competitive species – arrive to a site. Thus,

limits to diversity may shift from species and dispersal constraints early in succession to microsite availability and local competition later in succession, as predicted by the "successional shifting limitations hypothesis" ("SLH_{Succ}").

For my first chapter, I test the relevance of the SPH and NLH in limiting diversity, in addition to testing how the importance of these factors may shift over gradients of 1) productivity (SLH_{Prod}) and 2) time (SLH_{Succ}). I manipulate constraints imposed by seed availability and dispersal abilities to simulate different degrees of dispersal by adding multi-species seed mixtures at the onset of succession, and soil fertility/productivity by annually adding nutrient fertilization; and I track diversity over the first 11 years of succession. These treatments allow me to investigate the effects of species availability and soil fertility gradients on species coexistence and diversity throughout community development.

Acquiring better understanding of the forces governing plant diversity and community structure may provide insight into community organization of other heterotrophic organisms. For example, plant diversity and community structure (*i.e.* bottom-up forces) are thought to strongly influence organisms at higher trophic levels, for characteristics of plant communities largely determine food resources and habitat structure for other organisms (Chesson, 2000; Gause, 1934b; Greenwood, McIntosh, & Harding, 2010; Hutchinson, 1959; Novotny et al., 2006). Alternatively, top-down pressures of predation and parasitism may influence diversity and abundance of prey (Carter & Rypstra, 1995; Mooney et al., 2010; Schmitz, 2003; Schmitz, Beckerman, & Obrien, 1997), create self-regulating feedback loops (Bayliss & Choquenot, 2002; Kraus & Vonesh, 2010; Levins & Schultz, 1996), and indirectly affect plant community structure and productivity (Mooney et al., 2010). The influence of top-down forces on consumer communities may be mediated by bottom-up processes (Gruner, 2004; Sipura, 1999),

emphasizing the important role of local conditions in regulating consumer dynamics and structuring communities.

Diversity of basal resources – one type of bottom-up force – is hypothesized to determine diversity at higher trophic levels ("resource diversity hypothesis", "RDH") (Gause, 1934b; Hardin, 1960; Tilman, 1986). In support of the RDH, experimental augmentations of resource/plant diversity have been found to increase consumer diversity (Armbrecht, Perfecto, & Vandermeer, 2004; Haddad et al., 2009; Siemann et al., 1998), and in natural systems, consumer diversity shares a positive relationship with plant diversity (Southwood, Brown, & Reader, 1979). Along these lines, models predicting plant diversity may also be able to predict diversity at higher trophic levels; for example, if consumer diversity tracks resource diversity, the DEM (Huston, 1979, 1994) would predict consumer diversity to be highest at conditions of moderate productivity with low disturbance and/or high productivity with moderate disturbance.

However, it is important to consider co-varying relationships of plant diversity and productivity when forecasting effects of resource characteristics on consumer communities. Increased resource abundance (*i.e.* plant productivity) independent of changes to plant diversity is hypothesized to promote consumer diversity and abundance ("resource abundance hypothesis", "RAH") (Abrams, 1995; Srivastava & Lawton, 1998). Yet, if plant diversity is dependent on productivity as predicted by the unimodal plant diversity-productivity curve, consumer responses to augmented productivity may vary with corresponding reductions or increases in plant diversity. In addition to effects of plant diversity and abundance, composition and density of plant litter (Hansen, 2000) and plant species composition (Schaffers et al., 2008) have been found to influence consumer community structure, suggesting additional plant-based factors to influence consumers.

While plant-based resources are expected to be influential in the assembly of consumer communities, dispersal of organisms across a landscape can influence the distribution of consumers among connected communities (*i.e.* metacommunity ecology: Leibold et al., 2004; Holyoak, 2005). In addition to environmental factors, spatial processes, such as dispersal dynamics and source-sink dynamics (Mouquet & Loreau, 2003), may influence consumer community structure across a landscape (Cottenie, 2005). Therefore, spatial processes must be included when testing the relative influence of alternative factors shaping consumer communities.

In my second chapter, I investigate the relevance of local bottom-up processes in shaping consumer community structure by testing predictions of the RDH, DEM, and RAH, in addition to exploring influences of plant species composition and litter density. Additionally, I evaluate the relative influence of spatial processes *versus* local conditions in determining consumer communities. I sample arthropod communities in a tract of managed grassland, which over the past decade has undergone the following experimental treatments: sowing of native prairie seeds, nitrogen fertilization, and haying disturbance. These treatments have resulted in divergent plant communities, ranging from highly diverse assemblages containing many native prairie forbs and warm-season grasses, to low diversity assemblages containing mostly non-native cool-season grasses. In the year of arthropod sampling (2011), I compare patterns of arthropod community structure to plant community structure to determine if arthropods respond to alterations of resource-based characteristics of the plant community (*e.g.* diversity, composition, *etc*). Also, I conduct multiple regression and variance partitioning analyses to determine the amount of variation in arthropod diversity, abundance, and composition explained by plant community structure, direct effects of experimental treatments, and spatial processes. In addition to

examining whole community responses, I examine arthropod responses within three nested assemblages of the arthropod community (aerial arthropods, substrate-dwellers, and vegetation-dwellers) in order to identify niche-specific drivers of consumer community structure.

CHAPTER 1: Species availability and soil fertility interact to govern plant diversity across gradients of productivity and successional time

INTRODUCTION:

Understanding patterns of diversity and community development through secondary succession has been of interest for many decades (Bazzaz, 1975; Huston & Smith, 1987; Inouye et al., 1987; Odum, 1969; Tilman, 1987), as has the pursuit to understand mechanistic drivers underlying successional patterns (Bazzaz, 1979; Connell & Slatyer, 1977; Tilman, 1985, 1990). Succession results from a variety of mechanisms, most of which are not mutually exclusive (Huston & Smith, 1987; Odum, 1969). A particularly important mechanism of succession, the colonization-competition trade-off (Tilman, 1994), encapsulates the interplay of two dominant drivers of community dynamics: dispersal/colonization and competition (Tilman, 1994). Here, a trade-off among species in ability to compete for resources and ability to disperse to and colonize a site can drive successional turnover in species composition and dominance (Gleeson & Tilman, 1990; Tilman, 1990, 1994). Alternative models of succession propose other factors to drive compositional turnover, such as life history traits (*e.g*. longevity, growth rate, latency to germination, resource use) (Ben-Hur et al., 2012; Connell & Slatyer, 1977; Egler, 1954; Tilman, 1985), modification of the environment by early colonists (*i.e.* the facilitation model: Clements, 1936, Connell & Slatyer, 1977), and through feedback dynamics between soil microorganisms and host plants (De Deyn et al., 2003; Reynolds et al., 2003). These varied models of succession are, again, not mutually exclusive and will be relatively more or less influential depending upon characteristics of the developing system of interest (Connell & Slatyer, 1977; Platt & Connell, 2003).

How can species turnover through succession translate to temporal patterns of diversity? Although a variety of patterns have been observed, most studies of secondary succession have shown a strong increase in species richness over early succession, followed by a slowing of species accumulation or even a decline in later years in some cases (Bazzaz, 1975; Bonet & Pausas, 2004; Wang, Shao, & Shangguan, 2010). Several different processes could give rise to these common successional patterns. Limitations to plant species richness at different times and places may range from the effects of abiotic stress and individual-based interactions resolved at small scales, to processes that operate at field-, landscape-, and regional-scales determined by species pools available for colonization (Caley & Schluter, 1997; Cornell & Lawton, 1992; Cornwell & Grubb, 2003; Huston, 1999; Lawton, 1999; Ricklefs, 1987; Tilman, 1997). The size of the regional species pool can constrain the number of species available to a site that are suited to a local environment, and thus limit a site's potential richness (Taylor et al., 1990; Partel et al., 1996; Zobel, 1997). Additionally, proximity of a site to local seed sources and differential dispersal ability among available species can influence rates of species arrival and timing of establishment for particular species (Eriksson, 1993; Nathan & Muller-Landau, 2000; Taylor et al., 1990). The "species pool hypothesis" ("SPH": Taylor et al., 1990; Eriksson, 1993; Zobel, 1997) predicts limitations imposed by species pools, propagule availability, and species' dispersal abilities to dominantly constrain the richness of local communities, regardless of environmental conditions or stage of community development. Alternatively, the "niche limitation hypothesis" ("NLH": Tilman, 1982; Tilman & Pacala, 1993) predicts richness to be most constrained by niche dimensionality of the local habitat as determined by the abiotic environment, the absolute and relative availabilities of resources, and by the outcome of local species interactions. It is implicit to the NLH that species pools and species availability to sites

are non-limiting to species richness, regardless of a site's position along an environmental gradient or stage of community development.

Species richness has been found to be limited by constraints predicted by both the SPH (*e.g.* Caley & Schluter, 1997; Foster & Tilman, 2003) and NLH (*e.g.* Tilman, 1993; Crawley et al., 2005; Pierik et al., 2011), yet such limitations are not mutually exclusive. Thus, an important current goal in community ecology is to better understand how the relative importance of these differently-scaled constraints on species richness vary with stage of community development (Mouquet et al., 2003; Munguia, 2004) and along environmental gradients (Foster, 2001; Foster et al., 2011; Houseman & Gross, 2006; Klanderud, 2010). For example, both seed availability and local microsite availability are known to limit colonization rates and species richness during early (Clark et al., 2007; Eriksson & Ehrlen, 1992; Foster & Dickson, 2004; Foster et al., 2007; Zobel et al., 2000) and late (Dybzinski & Tilman, 2012) stages of community development, yet the relative importance of either factor over the course of succession is unknown. The importance of seed/dispersal limitations and microsite availability may shift over a successional gradient, particularly if there is a trade-off between dispersal ability and competitive ability among species in the species pool (Tilman, 1994). Early in succession, initial colonists with strong dispersal abilities arrive from external sources or emerge from seed banks in the soil to exploit abundant and largely uncontested resources in open microsites. Strong competitors (mid- to late-successional species) gradually overcome species pool/dispersal constraints (Tilman, 1994) to arrive to a site and increase in abundance, leading to stronger competitive interactions in highly contested microsites and greater importance of competitive exclusion as a limit to local diversity. Based on these expected temporal patterns, the "successional shifting limitations hypothesis" ("SLH_{Succ}") predicts limitations to species richness to shift over succession, from

constraints imposed primarily by dispersal (Tilman, 1994) and local species pools, *i.e.* seed banks and nearby external seed sources (Tofts & Silvertown, 2002; Turnbull et al., 2000), to constraints imposed by microsite availability and competitive exclusion. The SLH_{Succ} then would give rise to the common temporal patterns of species richness over succession discussed above, with dispersal constraints and delayed arrival producing the early accumulation of diversity but increasing competition intensity later leading to reduced rates of species accumulation and eventual community saturation. However, it is important to note that an observed saturating or unimodal relationship between species diversity and time does not by itself indicate competitive saturation of diversity. The SPH_{Succ} in fact could produce a saturating relationship as a result of species spool exhaustion – which would cause diversity to level off at a level below that set by local microsite and niche availability.

In addition to successional gradients, diversity has long been known to vary along gradients of soil fertility and productivity, yet the processes that generate and maintain these patterns are continually disputed (Abrams, 1995; Adler & Collins, 2011; Waide et al., 1999). At local scales, diversity is often hypothesized to share a unimodal relationship with productivity (Huston, 1994; Mittelbach et al., 2001; Rosenzweig, 1995), peaking at intermediate levels of productivity and declining as productivity either increases or decreases. In addition, the fertilization of plant communities with nutrients, particularly nitrogen, consistently leads to increased production and decreased diversity (Carson & Barrett, 1988; Tilman, 1987; Tilman, 1993). Declines in plant diversity at high fertility and productivity have often been attributed to increased competitive exclusion by dominant species (NLH: Foster et al., 2004). However, it has been suggested that declines in diversity at high productivity could be at least partially due to a limited pool of species adapted to high productivity habitats that could take the place of

displaced species (SPH: Taylor et al., 1990; Huston, 1999). Process limiting diversity could also vary along fertility and productivity gradients, as predicted by a productivity-based version of the shifting limitations hypothesis ("SLH_{Prod}"). The SLH_{Prod} predicts that the number of species able to coexist at a site is most limited by species pools and dispersal constraints at low to moderate levels of productivity, and, as productivity increases, increasing rates of competition and risk of competitive exclusion under decreasing microsite availability shift control of species coexistence to local processes (Cornell & Lawton, 1992; Foster et al., 2004; Grime, 1979; Huston, 1994, 1999; Lawton, 1999). Productivity – defined here as energy flow through a system – generally increases from early to mid-succession (Wang et al., 2010), suggesting that constraints to community diversity mediated by productivity (SLH_{Prod}) may vary over successional time, and be most relevant during mid- to late-succession when competitive species occur at high densities and pressures of local competition and exclusion may be more important. Yet, interactive effects of soil fertility/productivity and successional gradients on community development and diversity are relatively unexplored (*but see* Guo, 2003).

Predicting how regional processes interact with environmental conditions and how local species interactions govern species coexistence and diversity has become an common goal of numerous short-term ecological studies (Dickson & Foster, 2008; Eriksson & Ehrlen, 1992; Foster, 2001; Foster & Dickson, 2004; Gross, Mittelbach, & Reynolds, 2005; Houseman & Gross, 2006; Klanderud, 2010; Myers & Harms, 2011; Tilman, 1997). Yet, these studies only track short-term (*i.e.* 1-5 years) diversity patterns in established communities (*e.g.* old-fields with pre-existing vegetation) subject to modest – or no – disturbance. Because the size and intensity of disturbances can influence re-colonization rates and compositional trajectories through succession (Platt & Connell, 2003; Rogers & Hartnett, 2001), the roles of seed availability and

local environmental conditions in limiting diversity should also be examined in communities at the onset of re-colonization and development, *i.e.* following intensive, community-wide vegetation removal and soil disruption.

Here we present results from a long-term field experiment to test the roles of species availability and local microsite/niche limitation in constraining plant diversity in an abandoned old-field system in northeastern Kansas, and examine how the importance of these factors may shift over a successional gradient and soil fertility/productivity gradients. We experimentally manipulated the availability of mid- and late-successional species to plots at the onset of succession using multi-species seed additions, and manipulated productivity and the availability of soil nitrogen (N) and phosphorus (P) throughout succession via annual fertilization. By tracking plant diversity responses over the first eleven years of secondary succession, we address: 1) to what extent is plant diversity limited by seed availability versus soil resource supply and productivity; 2) do these factors and the interaction of the two vary in their influence on species diversity over the course of secondary succession; 3) which hypotheses (NLH, SPH or SLH) are most applicable to understanding the regulation of plant diversity along gradients of succession and soil fertility/productivity?

We first test if constraints of species availability and dispersal, and/or constraints of local niche availability and local competition determine local diversity. If so, we expect diversity to increase in response to seed addition regardless of soil fertility level (in support of constraints of species availability and dispersal, as predicted by the SPH) and/or diversity to decline in response to increased soil nutrient availability regardless of sowing level (in support of effects of niche limitation and competition, as predicted by the NLH). If the aforementioned limitations shift in importance over time as predicted by SLH_{Succ}, we expect effects of sowing of mid- to

late-successional species to be strongest early in succession and to diminish over time (Fig 1.1). If local productivity and competition mediate the importance of seed availability in constraining diversity, we expect positive effects of seed addition on diversity to be strongest in sites of low soil fertility and low productivity/competition, and for these effects to dampen with increasing soil fertility and productivity/competition, as predicted by SLH_{Prod} (Fig 1.1). Lastly, if the availability of competitive species mediates the importance of productivity-driven constraints to diversity (*i.e.* those predicted by the SLH_{Prod}), we expect effects of the soil fertility/productivity gradient on diversity to emerge once mid- to late-successional species become abundant at a site (*i.e.* upon sowing in sown plots; after dispersal constraints are overcome in non-sown plots) and competitive exclusion is important (Fig 1.2).

MATERIALS & METHODS:

Study site and experimental design

This study was conducted at the University of Kansas Field Station (KUFS), located in northeastern Kansas along the deciduous forest-tallgrass prairie ecotone. Prior to experiment establishment, this site was historically hayed and, upon abandonment, became dominated by the non-native C_3 grasses, *Bromus inermis* and *Schedonorus phoenix* (Foster et al., 2011).

In 2000, we established a long-term factorial field experiment at the site manipulating the supply of soil N and P, and the seed availability of mid- and late-successional plant species to an array of 96 permanent plots. To prepare the site, an area of approximately 70 × 120 m was sprayed with glyphosphate herbicide in summer 2000, and was ploughed and disked multiple times through March-April 2001. In April 2001 we established six 10 × 62 m rectangular blocks on the site. Each block contained two 10 × 26 m main-plots, and each main-plot contained eight

4 × 5 m plots, for a total of 96 experimental plots (Figure 2). Adjacent blocks were separated by 12-m buffer strips, main-plots by 10-m strips, and plots by 2-m strips. We established a factorial treatment regime consisting of 16 unique treatment combinations (N = 6) using a blocked, split-plot design. We randomly assigned the two main-plots within each block to one of two levels of experimental multi-species seed sowing, with seeds of 53 plant species (Table I) experimentally added ("sown") or not added ("not sown"). Within each main-plot, we crossed two plot-level factors in a 4 × 2 manner; we administered four levels of nitrogen fertilizer (0, 4, 8, and 16 g N m^{-2} yr^{-1}) as ammonium-nitrate and two levels of phosphorus fertilizer (0 and 8 g P m^{-2} yr^{-1}) as super-phosphate.

Starting in 2002 we added nitrogen and phosphorus fertilizers to plots by applying half of the total added fertilizer in April/May and applying the remaining half in June each year. To administer the sowing treatment, we sowed seeds of 42 native and 11 naturalized exotic species (Table I) by hand to plots in April 2002 and 2003. Seed used in the experiment were obtained from several different regional seed suppliers. All sown species were present in the regional pool, and were represented in populations present in nearby old-fields and prairie remnants. The sown species represent a range of functional groups and include species of mid- to late-successional status. Seeds were added at relatively high rates (ranging from 100 to 320 seeds per species m^{-2} yr^{-1}, depending on availability) to saturate sites with seed, and not to mimic natural seed rain. Our goal here was to remove constraints to species recruitment and establishment early in succession imposed by dispersal and seed limitations.

Data collection and analysis:

To assess community diversity over the study period, we conducted visual cover surveys in mid-season (late-June/early-July) from 2002 to 2012. In each experimental plot we sampled

all vascular plants within two permanent 1 × 1 m sampling quadrats by enumerating all species present and their abundances. To acquire integrative measures of plot diversity, we combined species lists across the two quadrats and averaged each species' abundance across both quadrats. We then calculated species richness, Shannon's diversity, and evenness for each plot for each year. To estimate site productivity, we clipped aboveground biomass using electric clippers along one 2 × 0.8 m strip within each plot from 2002 to 2012. We partitioned biomass into live and litter portions, and measured the mass of the live portion (g m^{-2}) to estimate annual plot productivity.

To explore how seed and nutrient additions affect community diversity and productivity and how these effects vary by year, we constructed a repeated measures blocked, split-plot ANOVA for each response variable (species richness, evenness, diversity, and live biomass). We treated sowing as a between-subjects factor, N and P levels as split-plot factors, and year of sampling as a repeated measures (*i.e.* split-split plot) factor. We did not adjust for multiple comparisons due to the marginal number of response variables tested (N = 4). Upon detection of a significant interaction between year, sowing, and N on species richness, we conducted individual ANOVAs on species richness within each year to better test if and how the strength of sowing effects vary along a soil fertility (N) gradient (SLH_{Prod}). Again, we included sowing as a between-subjects factor, and N and P levels as within-subjects factors. Evenness, Shannon's diversity, and live biomass were – respectively – cubed, squared, and cube-root transformed to correct non-normally distributed data. We conducted statistical analyses in the R 2.15.1 base package (2012) and graphed our results using the R package 'ggplot2' (Wickham, 2009).

RESULTS:

Effects on biomass

Aboveground biomass varied significantly with year (year effect: Table II) and exhibited considerable variation over the study period (Fig 3). Biomass production increased with increasing levels of N (N effect: Table II) and, to a lesser extent, P (P effect: Table II). The strength of positive N effects varied by year, with the strongest effects occurring in 2003, 2005, 2008, and 2010 (year × N interaction: Table II; Fig 3). Stronger effects of N on biomass occurred in non-sown than sown plots (sowing × N interaction: Table II; Fig 3). Seed addition consistently increased aboveground biomass over the study period (sowing effect: Table II), but the magnitude of this positive effect varied by year (year × sowing interaction: Table II; Fig 3) and with N level (year × N interaction: Table II; Fig 3).

Effects on species richness, evenness, and diversity

Measures of species richness, evenness, and diversity varied significantly with year (year effects: Table II), indicating strong changes in community structure over time. During the first few years of the study period (2002-2004), all sites experienced large species gains and early peaks in species richness, yet rates of species gains and peak species richness were much greater in sown than non-sown plots (Fig 3). Following this early peak, species richness declined and eventually leveled off; but, again, rates of decline and magnitude of species loss were greater in sown than non-sown plots (Fig 3). Despite greater declines in richness over time, sown plots were consistently more species rich than non-sown plots over all levels of N (Fig 3), and contained overall greater occupancy of sown species than non-sown plots (Table I). Additionally, patterns of species evenness and diversity over time varied between sowing treatments. Non-sown plots experienced early increases in evenness and diversity (2002-2004), followed by

declines (2005-2008), and subsequent inclines (2009-2011/2012). Unlike this undulating pattern, sown plots exhibited asymptotic trends in evenness and diversity (Fig 3).

Seed addition consistently increased species richness and Shannon diversity (sowing effects: Table II, Fig 3). The strength of positive sowing effects on richness and diversity varied by year (year × sowing interactions: Table II), with the strongest effects on richness occurring in earlier years (2003-2007) and then declining in magnitude over time. In contrast, the strongest effects of sowing on Shannon diversity occurred in later years (2004-2010) (Fig 3). The directionality of sowing effects on evenness varied by year, with negative effects appearing in early years (2002-2004) and positive effects appearing later (2005-2012) (year × sowing interaction: Table II; Fig 3).

Species richness generally declined with increasing levels of added N (N effect: Table II), but the strength of this effect varied both by sowing level and year (year × sowing × N interaction: Table II). Among sown plots, negative effects of N appeared early on and were strongest between 2003-2005 and 2008-2011; whereas, in non-sown plots, negative effects of N were generally weaker in magnitude (compared to sown plots) and appeared later in the study period (2008-2012) (Fig 3). Separate, within-year ANOVAs revealed significant sowing × N interactions in three years: 2005 ($F = 5.212$; $p = 0.0051$), 2008 ($F = 9.623$; $p = 0.0001$), and 2010 ($F = 7.461$; $p = 0.0007$). For all three years, positive effects of sowing were weakest among sites subjected to the highest level of N addition (16 g N m^{-2} yr^{-1}) compared to sites with lesser concentrations of N (Fig 4).

Early on, effects of N on evenness were weak and occasionally positive, whereas stronger, negative effects of N addition appeared in later years (year × N interaction: Table II; Fig 3). Negative effects of N on Shannon's diversity were consistently stronger in later years

(year × N interaction: Table II; Fig 3). Negative effects of N on both evenness and diversity were stronger in sown than non-sown plots, and were similar in all years (sowing × N interactions: Table II). The strength of positive seed addition effects on evenness and diversity varied with N level; seed addition increased evenness and diversity most in plots with 0 and 4 g N m^{-2} yr^{-1} added, slightly less so in 16 g N m^{-2} yr^{-1}, and least in plots with 8 g N m^{-2} yr^{-1} added (Fig 5).

Overall, phosphorus addition reduced species richness (P effect: Table II). The strength of this negative effect was marginally greater in later years (year × P interaction: Table II) and marginally greater in sown plots (sowing × P interaction: Table II) (Fig 6). For species evenness and diversity, effects of P addition were contingent on sowing and N levels (N × P × sowing interaction: Table II). Among non-sown plots, P addition decreased evenness and diversity in plots at intermediate levels of N (plots with 4 and 8 g N $m^{-2}yr^{-1}$: Fig 6). However, among sown plots, P addition decreased evenness and diversity in plots with 16 g N $m^{-2}yr^{-1}$ only (Fig 6).

DISCUSSION:

Through this study, we find that species availability and local processes strongly influence community diversity over the course of secondary succession, and that the strength and nature of these forces interact and vary over time. Experimental sowing of mid- and late-successional species early in succession revealed strong constraints of seed availability and dispersal limitation on diversity – consistent with the SPH – and altered temporal patterns of colonization and species accumulation considerably. Positive effects of seed addition on species richness attenuated with successional time, suggesting that limits to species coexistence may shift from seed availability to microsite availability and competitive interactions over time, as predicted by the SLH_{Succ}. Nitrogen enrichment generally reduced species richness, evenness, and

diversity, which is consistent with the NLH and findings from numerous past studies (Dickson & Foster, 2011; Harpole & Suding, 2011; Tilman, 1993; Wilson & Tilman, 2002). The magnitude of N effects on richness and their timing in succession were contingent on sowing treatment, indicating that species pools and dispersal limitations of late successional/competitive species can mediate effects of resource gradients on species coexistence. Additionally, positive effects of seed addition on species richness, evenness, and diversity were dampened under high levels of N fertilization, suggesting that constraints to diversity shift from seed and dispersal limitations at low soil fertility/productivity, to control by local competition and microsite availability at high soil fertility/productivity, in support of the SLH_{Prod}. Our study emphasizes the importance of both species availability and local soil fertility/competition on diversity, as well as the contingencies of these effects through successional time and across local productivity gradients. Our findings are especially pertinent to understanding processes governing species re-establishment and dynamics of diversity in early stages of community development.

We test the importance of species availability and dispersal, and local resource conditions and niche dimensionality on diversity following a community-wide disturbance, and explore temporal contingencies of these factors. All plots at our study site – both sown and unsown – experienced immediate species gains (mean richness of non-sown plots in 2002: 18.04; mean richness of sown plots in 2002: 25.65), suggesting that high microsite availability following a community-wide disturbance promotes colonization and species gains early in succession. Additionally, seed addition immediately and persistently increases species richness across all soil fertility levels (Fig 3), and eventually leads to increased community evenness and diversity (Fig 3). These positive effects of sowing are consistent with past demonstrations of seed limitation of diversity in plant communities (Foster & Dickson, 2004; Foster et al., 2004; Foster & Tilman,

2003; Tilman, 1997; Zobel et al., 2000). Notably, strong positive effects of sowing persist over long periods of community development, indicating that communities cannot completely overcome diversity constraints imposed by seed and dispersal limitations even over extended time periods. Long-term positive effects of propagule addition are consistent with work in other systems (Foster et al., 2007; Foster & Tilman, 2003; Tilman, 1997; Zobel et al., 2000), but, to our knowledge, this study reveals sowing effects exceeding the duration of any other seed manipulation study.

In our study strong increases in richness in response to sowing in early succession diminished over time; this pattern is consistent with competitive exclusion becoming progressively more important than species availability in constraining coexistence, as predicted by the SLH_{Succ}. However, there are alternative explanations for these declines. One answer is that most of these species losses in sown plots were from among sown species that never became abundant (data not shown). These losses may result from stochastic extinction associated with small initial population size of rare species or the failure of some species to persist under prevailing abiotic conditions, possibly stemming from high mortality among vulnerable juveniles. An alternative explanation may be that sowing effect size may have attenuated due to exhaustion of the added species pool; as added seeds germinated and either established or failed to, progressively fewer viable seeds remained in the added pool, therefore reducing the likelihood of colonization/establishment by added seeds of sown species – and possibly reducing sowing effect size – with time since seed addition. Overall, diminishing sowing effect strengths may reflect shifting limits to diversity over succession (SLH_{Succ}) or the aforementioned alternative mechanisms, calling for further inquiry into the strength of seed/dispersal constraints to diversity through succession.

In successional systems, species richness often increase over in early succession but subsequently levels off or even begins to decline (Bazzaz, 1975; Bonet & Pausas, 2004; Dyrness, 1973), as found here. Interestingly, temporal patterns of richness seen here depend on both species availability and N fertilization level (Fig 3), which may relate to temporal differences in the arrival and establishment of highly competitive species and thus differences in the onset of competitive exclusion in response to soil nutrient availability. In general, mid- to late-successional species (*e.g.* native C_4 grasses and prairie forbs) outcompete short-lived, non-native species for resources (Tilman & Wedin, 1991; Wedin & Tilman, 1993) but may require more time to colonize a site than weaker competitors (Tilman, 1994). By experimentally removing colonization constraints of mid- to late-successional species via seed addition, we accelerate the accrual and dominance of competitive species in sown plots compared to non-sown plots, which are subject to natural seed rain and dispersal constraints (Table I). This acceleration of dominance by competitive species may increase the rate at which sown communities are driven by local competitive exclusion in comparison to non-sown communities. Thus, we may expect communities lacking strong competitors to be most constrained by species availability, and less so by local competition and soil fertility/productivity gradients; and for communities saturated with highly competitive species to be governed primarily by local competition and to respond to soil fertility/productivity gradients, and be less limited by species availability. At this site, seed and dispersal limitations have been found to limit deterministic species sorting and compositional differentiation across resource gradients (Foster et al., 2011), with communities subject to high species availability demonstrating stronger species sorting and community differentiation across a soil fertility gradient than communities subject to low species availability. Discrepancies in the strength of species sorting likely correspond to patterns of

diversity observed here, with delayed and relatively weak effects of soil fertility/productivity occurring when dispersal and species availability constraints are intact (*i.e.* in non-sown plots), and earlier and stronger fertility/productivity effects occurring in communities subject to high species availability and unrestricted dispersal (*i.e.* sown plots) (Fig 3). These discrepancies may indicate temporal differences between sowing levels in terms of when communities undergo a shift in dominant limitations to diversity – *i.e.* when the importance of microsite availability and local competition surpasses that of seed and dispersal constraints. Therefore, species availability and dispersal limitations can regulate the timing and strength of species sorting and community differentiation during secondary succession.

Patterns of species coexistence across environmental gradients and the expression of these gradients in terms of local diversity can depend on several characteristics of the species pool – such as size, functional diversity, and species traits – in addition to the availability of said species. For example, when more species are present in the regional pool, species adapted to local environmental conditions are more likely to be represented in the regional pool and will be able to disperse to and colonize a site (Foster et al., 2011; Fukami, 2004; Questad & Foster, 2008). Furthermore, the functional diversity of these available species can determine how many available niches can be partitioned and the number of species that can coexist. Along these lines, communities subjected to seed additions of functionally diverse species pools have been found to experience greater spatial turnover and – when environmental heterogeneity was increased through disturbance – greater species richness than communities sown with functionally redundant species (Questad & Foster, 2008). Here, we saturate recently disturbed communities with 53 species spanning multiple functional roles (Table I) and varying in functional traits pertaining to growth form, resource acquisition, and life history. Following our large-scale

disturbance, functionally diverse, sown species are able to exploit newly created niche opportunities and engage in trait-based species sorting along environmental gradients (Houseman & Gross, 2011) to a greater degree than species constrained by dispersal and availability in non-sown sites (Foster et al., 2011). Therefore, characteristics of the species pool in addition to constraints of species availability and dispersal are likely influential in determining local diversity along environmental gradients.

Patterns of reduced diversity with nutrient fertilization, as found at our study site (Fig 3 & 6), have been found in other successional grassland systems (Carson & Barrett, 1988; Foster & Gross, 1998; Tilman, 1987, 1993), and are hypothesized to result from amplified local competition under high productivity conditions (Huston, 1994; Tilman, 1993) . Nitrogen and phosphorus levels do not interact to influence species richness, suggesting that these nutrients additively reduce richness, consistent with the niche dimensionality hypothesis (Harpole & Suding, 2011; Harpole & Tilman, 2007). The niche dimensionality hypothesis predicts that a greater number of unique limiting nutrients promotes species coexistence by increasing resource trade-off opportunities (Harpole & Tilman, 2007). Here, N and P fertilization may increase the availability of these nutrients to the point of becoming non-limiting, thus reducing niche dimensionality and consequently, capacity for species coexistence.

Responses of species evenness and diversity to phosphorus additions are more complex; negative effects of phosphorus on evenness and diversity are contingent on both soil nitrogen concentration and seed availability (Fig 6). In non-sown plots we found that P addition reduced evenness and diversity at intermediate levels of N, and in sown plots we found that P addition reduced evenness and diversity only at the highest level of N (Fig 6). Effects of soil phosphorus availability on local diversity can vary depending on the relative dominance of resident species

and their respective mycorrhizal associations (Collins & Foster, 2009) and on concentrations of other limiting soil nutrients, such as nitrogen (Janssens et al., 1998; Tilman, 1985). Here, P alters relationships between evenness/diversity and N level, yet the interaction between N and P is contingent on the availability of mid- to late-successional species. Again, this interaction emphasizes the role of regional processes and dispersal constraints in mediating species coexistence and diversity, particularly across resource gradients.

As nutrient additions – particularly of nitrogen – increase biomass and decrease diversity, we can ask: does soil fertility mediate the importance of regional species pools to diversity, as predicted by the SLH_{Prod}? This question represents a reciprocal approach to the interpretation of interactions between species availability and soil fertility discussed above. Here, we find the strength of positive sowing effects on species richness, evenness, and diversity to be weakest at high soil nitrogen levels in some years (Fig 4 & 5), consistent with the SLH_{Prod} (Foster et al., 2004; Grime, 1979; Huston, 1994, 1999). For species richness, significant interactions between seed and nitrogen addition appear in 2005, 2008, and 2010: years in which plots subjected to the highest concentration of nitrogen fertilizer (hereafter referred to as "high fertility plots") – particularly those that were sown – were markedly more productive than other plots. In line with the SLH_{Prod}, exceptionally high productivity in high fertility plots in these years may have amplified local competition and rates of competitive exclusion to the point where the majority of sown species were restricted from colonizing and establishing. Species equitability and diversity of sown plots are lowest at high fertility, suggesting that the dominance of few species in these plots may inhibit colonists – specifically of sown species – from establishing and reaching potential growth due to competitive suppression, leading to minimal increases in species richness, evenness, and diversity in response to sowing, in line with the SLH_{Prod}.

In parallel with the SPH_{Prod}, the species-sorting paradigm (Leibold et al., 2004) of metacommunity ecology emphasizes the role of environmental or competitive gradients in determining community structure, and interactions between these gradients and species dispersal across habitat patches. Here, we find evidence for the SPH_{Prod}, which not only corroborates past work testing this particular hypothesis (Foster et al., 2004), but also suggests that limits to species richness in this system support the species-sorting paradigm. However, this interaction can be interpreted reciprocally (Fig 1), *i.e.* by emphasizing the role of the species pool in the expression of environmental gradients when examining changing magnitude of the interaction across the entire study period. Thus, the interpretation of this interaction depends on the temporal scale at which the interaction is examined, which highlights the importance of the consideration of temporal scale when examining processes spanning multiple spatial scales.

In summary, we find that the relative importance of local and regional processes varies over both space and time in systems undergoing secondary succession. We provide evidence for both the SLH_{Succ} and SLH_{Prod}, adding to the increasing recognition of locally mediated effects of regional processes (Dickson & Foster, 2008; Foster, 2001; Foster & Dickson, 2004; Houseman & Gross, 2006; Myers & Harms, 2009, 2011). Additionally, we find that seed availability and dispersal constraints mediate the temporal appearance and strength of effects of local resource availability and competition. The relevance of soil resource- and productivity-mediated controls of diversity appear to change over successional seres; thus, gradients in space and time likely interact to determine pertinent drivers of diversity throughout community development. Recognizing these interactions can aid in the interpretation of diversity patterns across multiple gradients – particularly those that are common and likely important, *i.e.* time and space – and

lead to better understanding of forces governing community development and diversity following large-scale disturbances.

TABLES & FIGURES:

Table I. List of plant species experimentally added to sown plots and each species' functional guild, origin († I – Introduced species; N – Native species), and occurrence. Occurrence is represented by mean plot occupancy (number of plots in which a species was present, averaged over all study years) and is listed for both non-sown ("NS") and sown ("S") plots (N = 48 plots for each sowing level).

			Mean plot occupancy	
Sown Species	Functional Guild*	Origin†	NS	S
Achillea millefolium	PF	N	0.09	2.00
Agastache nepetoides	PF	N	0.00	0.00
Amorpha canescens	PL	N	0.27	29.64
Andropogon gerardii	C_4-PG	N	0.91	24.36
Asclepias syriaca	PF	N	6.55	3.55
Asclepias tuberosa	PF	N	0.09	15.55
Astragalus canadensis	PL	N	0.00	4.36
Bouteloua curtipendula	C_4-PG	N	0.00	27.36
Chamaecrista fasciculata	AF	N	1.45	29.73
Dactylis glomerata	C_3-PG	I	0.00	2.09
Dalea candida	PL	N	0.00	17.45
Dalea purpurea	PL	N	0.00	15.27
Desmanthus illinoensis	PL	N	0.00	40.18
Desmodium canadense	PL	N	4.82	9.00
Echinacea pallida	PF	N	0.00	14.18
Elymus canadensis	C_3-PG	N	0.36	14.73
Eragrostis trichodes	C_4-PG	N	0.73	0.18
Eryngium yuccafolium	PF	N	0.00	12.18
Eupatorium altissimum	PF	N	10.09	9.55
Festuca ovina	C_3-PG	I	0.09	0.18
Genetiana alba	PF	N	0.00	0.00
Helianthus maximiliani	PF	N	0.00	18.36
Heliopsis helianthoides	PF	N	0.27	28.45
Hesperis matronalis	BF	I	0.00	0.82
Lespedeza capitata	PL	N	0.82	41.55
Leucanthemum vulgare	AF	I	0.00	9.45
Liatris pycnostachya	PF	N	0.00	3.18
Medicago sativa	PL	I	0.00	0.18
Melilotus officinalis	BF	I	0.36	10.00
Monarda fistulosa	PF	N	0.64	39.18
Oenothera macrocarpa	BF	N	0.45	7.27
Panicum virgatum	C_4-PG	N	0.09	22.00
Penstemon albidus	PF	N	0.00	27.64
Penstemon digitalis	PF	N	0.00	0.00
Phleum pratense	C_3-PG	I	0.18	0.09
Poa pratensis	C_3-PG	I	38.64	37.82

Ratibida columnifera	PF	N	0.00	0.00
Ratibida pinnata	PF	N	0.09	21.64
Rudbeckia hirta	PF	N	0.09	10.55
Salvia azurea	PF	N	0.73	39.36
Schizachyrium scoparium	C_4-PG	N	0.09	13.73
Silphium perfoliatum	PF	N	0.00	5.18
Oligoneuron rigidum	PF	N	0.00	11.64
Sorghastrum nutans	C_4-PG	N	0.82	28.00
Sporobolus cryptandrus	C_4-PG	N	3.55	3.91
Symphyotrichum novae-angliae	PF	N	0.00	6.27
Teucrium canadense	PF	N	1.09	1.45
Trifolium pratense	PL	I	0.09	14.36
Trifolium repens	PL	I	0.18	15.18
Tripsacum dactyloides	C_4-PG	N	0.27	1.91
Verbena stricta	AF	N	5.00	31.45
Vicia villosa	PL	I	0.00	4.36
Zizia aurea	PF	N	0.00	24.09

*Key to abbreviations: AF, annual forb; BF, biennial forb; PL, perennial leguminous forb; PF, perennial non-leguminous forb; C_3-PG, perennial grass with a C_3 photosynthetic pathway; C_4-PG, perennial grass with a C_4 photosynthetic pathway.

Table II. Sources of variation for species richness, evenness, diversity, and biomass. Sources of variation include year of sampling ("Year"), N g m^{-2} yr^{-1} ("N"), P g m^{-2} yr^{-1} ("P"), and sowing treatment ("Sow").

		Species richness		Evenness		Shannon diversity index		Live Biomass	
Source	d.f.	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Repeated measures effects									
Year	10	2988.4	271.29***	0.8212	72.755***	56.36	44.095***	52.25	39.634***
Sow × Year	10	824.1	74.811***	0.4596	40.718***	49.61	38.816***	4.02	3.052***
N × Year	30	56.9	5.161***	0.0229	2.027**	4.69	3.67***	2.60	1.971**
P × Year	10	20.3	1.842•	0.0033	0.291	1.58	1.233	0.96	0.730
Sow × N × Year	30	20.9	1.894**	0.0103	0.915	1.72	1.347	1.25	0.950
Sow × P × Year	10	4	0.359	0.004	0.358	0.41	0.324	1.42	1.075
N × P × Year	30	11.8	1.073	0.0106	0.941	1.24	0.974	1.28	0.973
Sow × N × P × Year	30	9.1	0.828	0.0069	0.611	0.65	0.512	1.11	0.844
Error(Year)	800	11		0.0113		1.28		1.32	
Within-subjects effects									
N	3	1407	49.427***	0.09789	4.915**	63.79	29.467***	76.21	38.131***
N × Sow	3	139.1	4.888**	0.09004	4.521**	14.68	6.783**	14.84	7.426***
Error(N)	30	28.5		0.01992		2.16		2.00	
P	1	211.86	19.019**	0.0212	1.938	1.52	0.942	15.128	7.506*
P × Sow	1	55	4.937•	0.17556	16.047**	18.287	11.333**	0.001	0.00
Error(P)	10	11.14		0.01094		1.614		2.016	
N × P	3	7.685	0.283	0.03375	1.778	3.877	1.734	3.71	1.583
Sow × N × P	3	16.569	0.61	0.08655	4.56**	9.059	4.053*	1.512	0.645
Error(N P)	30	27.179		0.01898		2.235		2.344	
Between-subjects effects									
Sow	1	44292	390.7***	4.366	53.01***	1710.7	99.89***	91.48	68.47***
Error(Sow)	5	113		0.082		17.1		1.34	
• $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.									

Figure 1. Conceptual diagram of alternative hypothetical interactions. As shown in Box 1, the relative importance of species availability is expected to vary over both successional time (declining as succession progresses, as predicted by the SPH_{Succ}) and a productivity gradient (declining as productivity increases, as predicted by the SPH_{Prod}). As shown in Box 2, the availability of competitive, mid- to late-successional species is expected to positively mediate the expression of soil fertility gradients. Compared to the productivity-based prediction of the importance of species availability in Box 1, the prediction in Box 2 represents a reciprocal interpretation of the interaction between species availability and local environment.

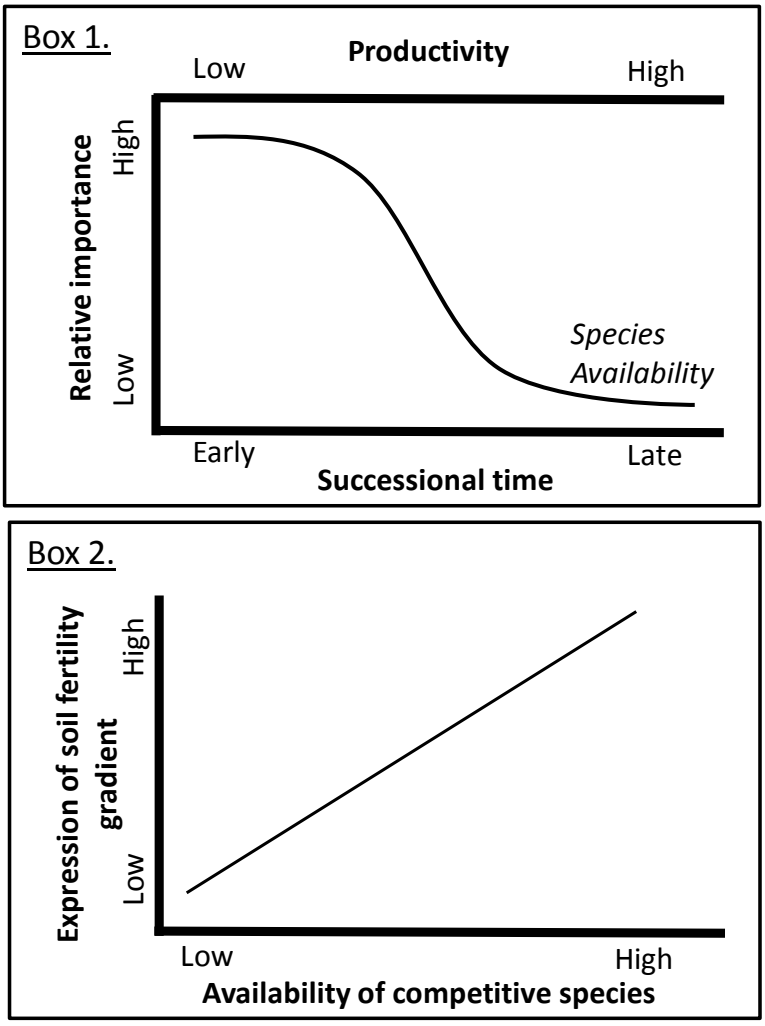


Figure 2. Experimental design of treatment regimes. The experiment consists of six blocks (separated by 12 m), with each block containing two main-plots (separated by 10 m), and each main-plot containing 8 plots (separated by 2m). The sowing treatment was applied at the main-plot level, and nitrogen and phosphorus fertilization treatments were applied at the plot level. See legend for treatment designations ('seeds' – sowing level; 'P' – phosphorus level: 0 or 8 gP m^{-2} yr^{-1}; Nitrogen level – gN m^{-2} yr^{-1} labeled within plots).

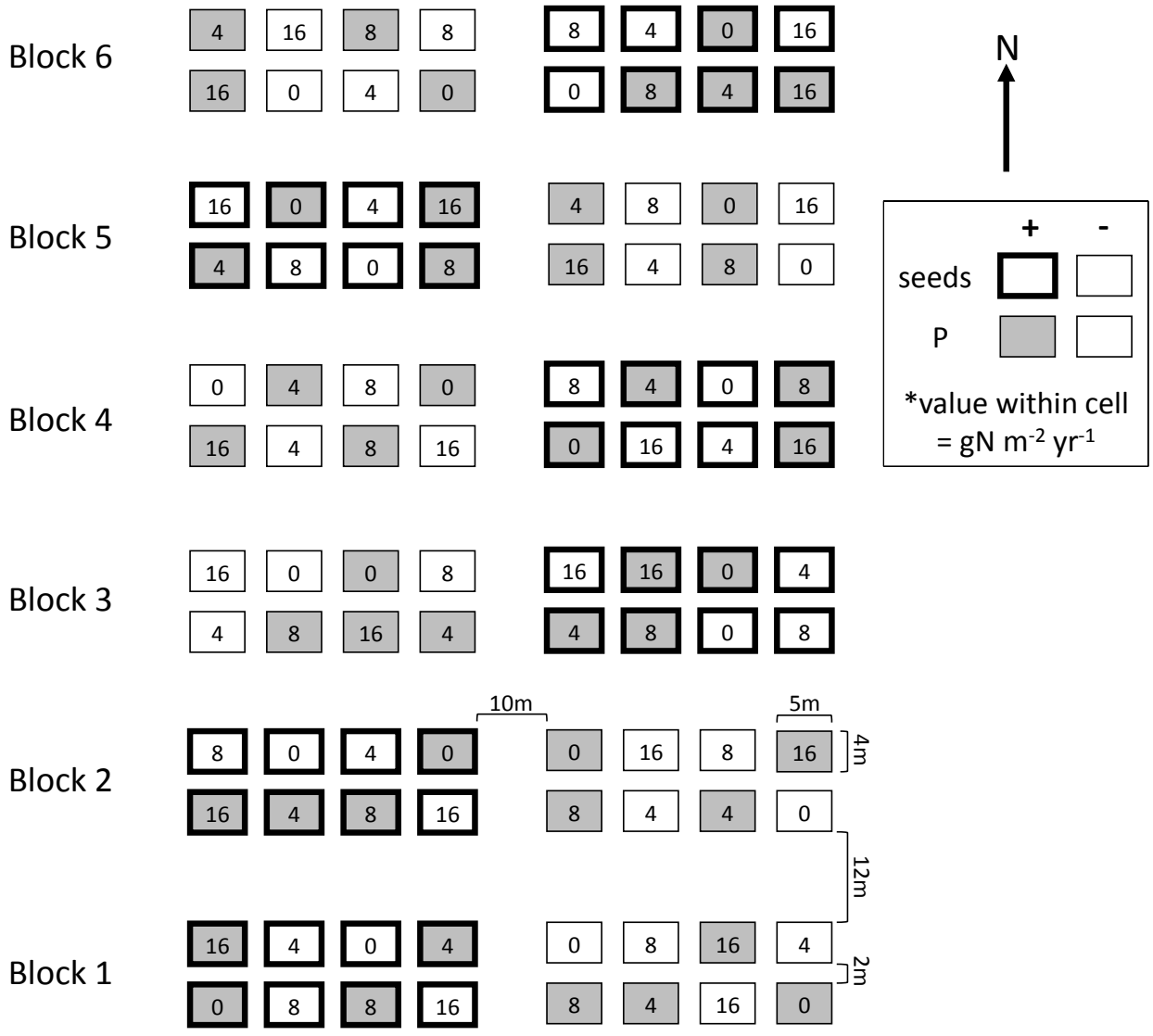


Figure 3. Effects of N level and sowing on plant species richness, evenness, diversity, and live biomass (means shown) over the study period. Significant main effects of nitrogen addition ("N"), sowing, and N × sowing interactions – in addition to interactions between year and these effects – for each response variable are listed to the right of each pair of graphs and labeled as labeled as: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

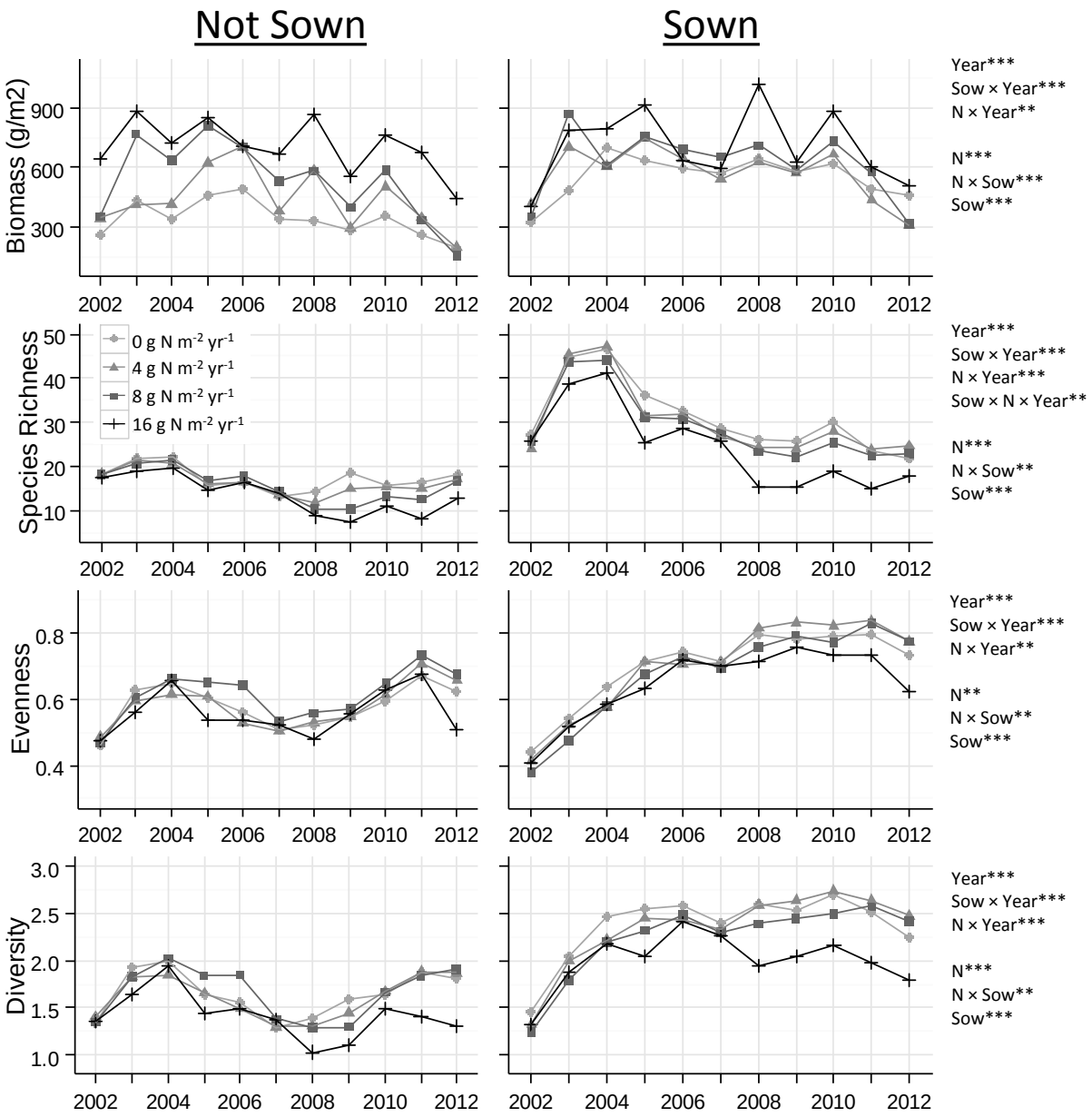


Figure 4. Interactive effects of N addition and sowing on species richness in years containing a significant year × sowing × N interaction ($p < 0.05$; means ± 1 SE shown). Note different scales for each year.

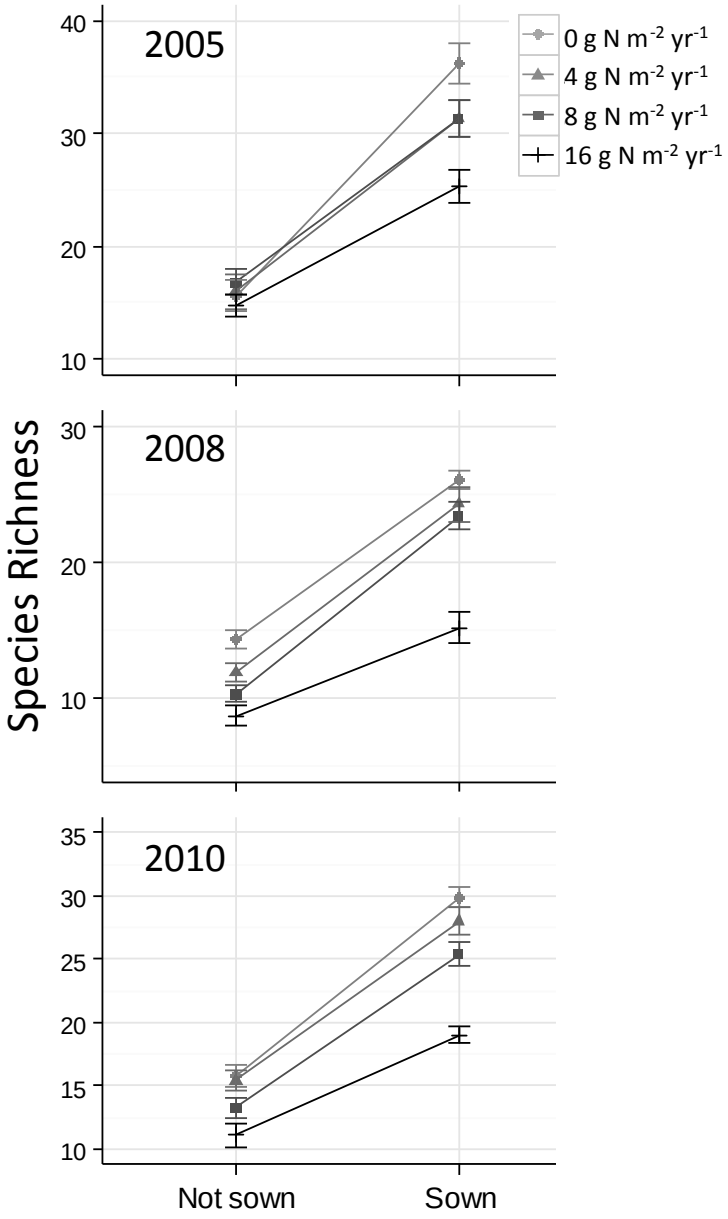


Figure 5. Interactive effects of N addition and sowing on overall evenness and diversity (means ± 1 SE shown).

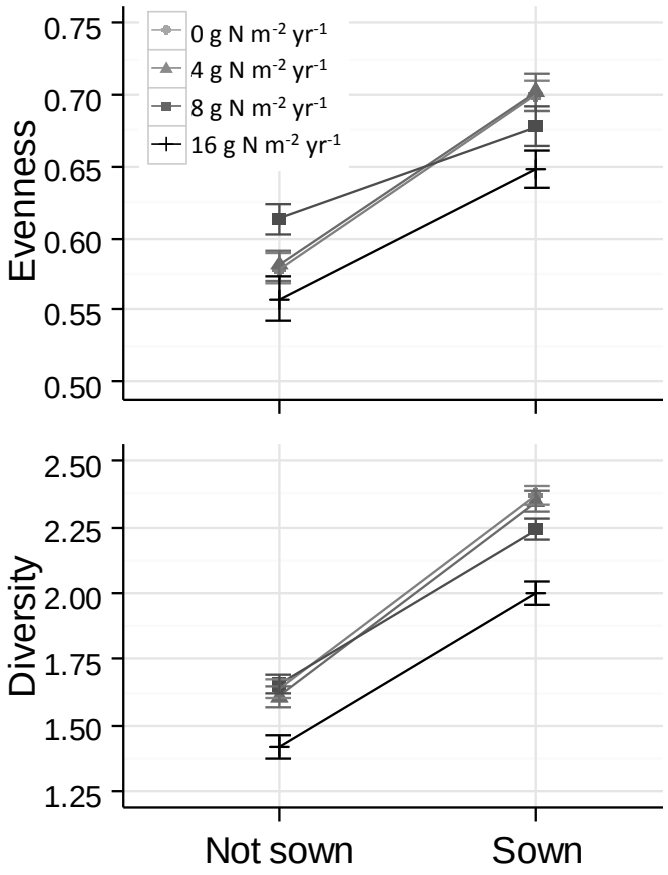
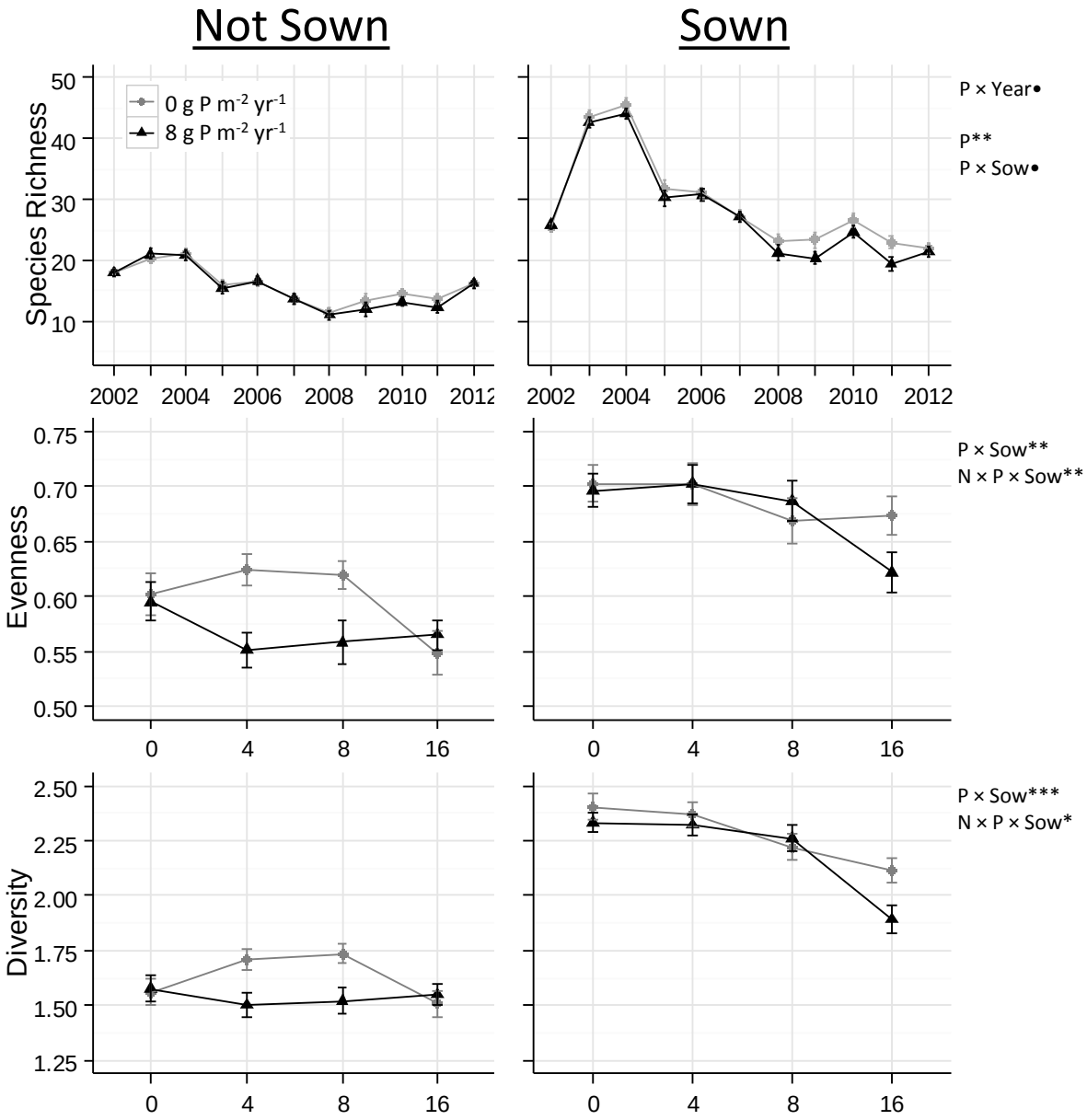


Figure 6. Effects of P addition, and N × P and P × Year interactions, on plant species richness, evenness, and diversity. The top row (means shown only) shows P and sowing effects for each year of sampling, whereas the bottom two rows (means ± 1 SE) show N × P × sowing interactions pooled over the study period. Significant effects are listed to the right of each pair of graphs and labeled as labeled as: •$p < 0.10$; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.



CHAPTER 2: Plant-based resources and spatial processes influence arthropod community structure in an old-field system

INTRODUCTION:

Tallgrass prairie (TGP) ecosystems harbor highly diverse and productive organismal communities (Samson & Knopf, 1994). In North America TGPs now cover only approximately 1% of their original range (Losey & Vaughan, 2006) due to wide-spread habitat destruction, urbanization, fire-suppression, and varied agricultural activity. Remaining native grasslands are subject to a wide range of anthropogenic forces that impact their composition, diversity and function, including varied management, habitat fragmentation, and spread of invasive species. Arthropod communities in TGP ecosystems are of high restoration priority; they provide important ecosystem services such as pollination, nutrient cycling, decomposition, and biological control (Whiles & Charlton, 2006) but are potentially experiencing extinction rates unmatched by other taxa (Thomas et al., 2004).

To better understand the impacts of anthropogenic disturbances and altered management on arthropod communities and to better inform active restoration of arthropod-mediated ecosystem services, we must first identify assembly processes and pressures shaping arthropod, or more generally, consumer community structure. Pressures of predation and parasitism (*i.e.* top-down forces) can control abundance and diversity of lower heterotrophs (Carter & Rypstra, 1995; Mooney et al., 2010; Schmitz, 2003; Schmitz et al., 1997), create self-regulating feedback loops (Bayliss & Choquenot, 2002; Kraus & Vonesh, 2010; Levins & Schultz, 1996), and indirectly affect plant community structure and productivity (Mooney et al., 2010). Alternatively, effects of nutrient availability to plants, abiotic environmental conditions, and habitat structure (*i.e.* bottom-up forces) affect consumer community structure by providing or altering sources of nutrition, habitat, and physiological stress (Grundel et al., 2010; Noordijk et al., 2010; Schaffers et al., 2008; Siemann, 1998); and likely mediate the extent of top-down control on consumer communities (Gruner, 2004; Sipura, 1999). In line with this bottom-up perspective, consumer

communities are hypothesized to assemble based on available resources, which depend on characteristics of the local plant community, *e.g.* plant species composition, diversity, *etc*. Because consumers occupying different niche space may utilize different sets of resources (Chesson, 2000; Hardin, 1960; Macarthur & Levins, 1967), examining responses of different consumer guilds (*e.g.* epigeic taxa, aerial taxa) or trophic levels (*e.g.* predators, herbivores) may unveil niche-specific drivers of community structure.

Generally, a more diverse resource base is assumed to support a more diverse set of consumers (Gause, 1934b; Hardin, 1960; Tilman, 1986); thus a diverse plant community should sustain a diverse set of herbivores, leading to a diverse set of predators, and so on – an idea which will be referred to hereafter as the "resource diversity hypothesis" ("RDH") (based on Chesson, 2000; Hutchinson, 1959; Novotny et al., 2006). If plant and consumer diversity are causally linked as predicted by the RDH, models of plant diversity may be used to predict the potential impacts of disturbance and altered availability of basal resources (water, nutrients) on community structure and diversity at higher trophic levels. The Dynamic Equilibrium Model ("DEM": Huston, 1979, 1994) has been a particularly influential model of plant community organization over the last three decades. Under the DEM, increasing soil fertility leads to higher growth rates among plant competitors, greater overall production and amplified rates of competitive exclusion that reduces plant diversity at the highest levels of fertility. However, plant diversity can be maintained under conditions of high fertility and productivity if disturbances periodically create microsites open to colonization and reduce the abundance and vigor of dominant species, slowing the competitive exclusion of subordinate species. Under this model, plant diversity is predicted to be highest in sites of low disturbance and low-to-intermediate productivity, or in moderately disturbed sites with high productivity. Is the DEM an effective model for understanding and predicting the effects of soil fertility/plant productivity and disturbance on consumer communities? If plant diversity is the dominant factor shaping consumer communities in line with RDH, we expect consumer diversity to track the diversity responses of plants to these factors.

Alternatively, independent effects of other factors may be more important in determining consumer diversity, such as varied productivity, altered plant composition, and vegetation structure. Increased plant productivity (*i.e.* consumer resource abundance) is hypothesized to increase consumer diversity from the bottom-up through the resource abundance hypothesis ("RAH"). This positive bottom-up effect could occur either by: 1) increasing the abundance of scarce resources (and, consequently, overall equitability of resource types), thus increasing rare consumer species and/or supporting additional consumer species (Abrams, 1995), or by; 2) increasing overall abundance of resources (regardless of resource diversity), thus increasing the overall abundance of arthropods and supporting additional species through a sampling effect (Srivastava & Lawton, 1998).

Understanding the relative roles of plant diversity and productivity on consumer communities is complicated by the fact that plant diversity and productivity co-vary, and their relationship can be non-linear. For instance plant diversity is hypothesized to show a unimodal dependence on plant productivity, peaking at intermediate productivity and declining to very low levels in the most productive plant communities where rates of competition are high (Mittelbach et al., 2001; Tilman, Wedin, & Knops, 1996; Waide et al., 1999). Here, if resource diversity is an important determinant of consumer diversity, modest increases in resource abundance associated with the addition of basal resources (*e.g.* fertilizer) may have opposite bottom-up effects on consumer diversity depending on whether the habitat in question is located on the low productivity (ascending) or high productivity (descending) portion of the unimodal plant diversity-productivity curve. A modest increase in productivity on the ascending portion of the curve could potentially enhance resource abundance to consumers without a concomitant reduction in resource diversity, thus maintaining consumer diversity. On the other hand, modest increases in productivity on the ascending side of the curve could lead to local extinction of plant species and thus declines in resource and consumer diversity.

Aside from diversity and productivity, other components of vegetation structure – such as plant litter – may shape consumer coexistence and community structure by modifying micro-environmental

conditions at the soil surface (Facelli & Pickett, 1991) and influencing the composition and abundance of detrital resources (Wardle et al., 2006). Under the "plant litter hypothesis" ("PLH"), increased litter density is expected to allow greater consumer diversity by increasing refuge and detrital resource availability for epigeal organisms, and by creating favorable microclimate conditions.

Due to the ubiquity of host specialization by consumers (particularly by herbivores: Bernays & Graham, 1988), shifts in plant species composition are hypothesized to induce shifts in consumer composition and/or diversity by determining the availability of specific niches filled by specialized consumers. The "plant composition hypothesis" ("PCH"), then predicts that shifts in plant composition will invoke shifts in consumer composition.

In addition to local environmental factors (*e.g.* resource diversity), dispersal abilities and spatial dynamics of consumers across a landscape or matrix of habitat patches (*i.e.* a metacommunity) may influence how local processes shape local community structure (Leibold et al., 2004). Communities spanning a diverse set of ecological systems have been found to be strongly structured by independent effects of both environmental processes and spatial organization (Cottenie, 2005), thus emphasizing the importance of including spatial processes in models of community assembly and structure.

In our study we explore potential drivers of consumer assembly by examining arthropod responses to long-term factorial manipulations of soil nutrients, haying, and native prairie seed sowing in a post-agricultural old-field system in northeastern Kansas. By the time of the current study (2011), plant assemblages had diverged by treatment over the course of the previous decade into communities ranging from high productivity, low diversity assemblages dominated by non-native C_3 grasses to lower productivity, high diversity assemblages dominated by native C_4 grasses and forbs (Foster et al., 2009). The resultant plant communities typify a range of grassland habitat types and management regimes common to the Great Plains region: old-fields; low diversity/high input cool-season hayfields: high diversity/low-input native hay meadows; restored prairie; and CRP habitat.

Work in earlier years at our experimental site has supported the DEM for the plant community (Foster et al., 2009), allowing us to test predictions from the DEM with respect to consumer diversity (*i.e.* consumer diversity will track plant diversity across productivity and disturbance gradients). Furthermore, past work has also found that the restoration of native prairie plants via seed sowing in non-fertilized sites increased plant diversity (Foster et al., 2009). This provides a novel additional means to test the RDH in the absence of the potentially confounding effects of fertilization and increased productivity. Here, we address the following questions: **1)** How do fertilization, haying disturbance history, and enhancements of plant diversity associated with prairie restoration impact arthropod diversity, abundance, and composition? **2)** Does arthropod diversity across experimental gradients conform to DEM? **3)** To what extent are arthropod community responses consistent with RDH, RAH, PLH, or PCH? **4)** Which are better predictors of arthropod community response: local resource characteristics (*e.g.* plant diversity, productivity, *etc*) or spatial processes? and **5)** Do different guilds of arthropods respond similarly to grassland management strategies, resource characteristics, and spatial processes? To address these questions, we first briefly summarize plant community responses to the experimental treatments as observed in 2011, a decade after the experiment was started and the year in which arthropods were sampled. We then analyze responses of the arthropod community and evaluate predictions associated with the DEM, RDH, RAH, PLH, and PCH (*see* Figure 1 *for predictions*). If the DEM is supported we expect to observe negative effects of fertilization on arthropod diversity, but to a lesser degree in hayed plots. If RDH is supported we expect arthropod diversity to conform to DEM and to generally show a positive relationship with plant diversity across the experiment even when controlling for other potentially confounding factors. After controlling for covariance with plant diversity and other potentially confounding factors, we determine if support exists for the RAH (positive relationships between arthropod diversity/abundance and plant biomass), PLH (positive relationship between arthropod diversity and litter biomass), and PCH (strong influence of plant composition on arthropod diversity, abundance, or composition). Additionally, we examine the extent to which responses are predicted by

spatial processes independent of resource-related effects, and how responses may vary among arthropods inhabiting different niche spaces, *i.e.* spatially distinct microhabitats.

MATERIALS & METHODS:

Study site and experimental design:

We conducted this study in a well-established, long-term experimental tract in northeastern Kansas at the University of Kansas Field Station (KUFS). KUFS lies along the deciduous forest-tallgrass prairie ecotone, with soils comprised of clay and silty loams. Historically, this study site was utilized as a cool-season hay meadow, then maintained by periodic mowing from 1987 to 1999. Prior to establishment of a grassland management experiment in 2000, the site was dominated by two introduced C_3 grasses, *Bromus inermis* and *Lolium arundinaceum*, in addition to the following ubiquitous species: *Poa pratensis* (introduced C_3 grass), *Andropogon virginicus* (native C_4 grass), and *Solidago canadensis*, *Eupatorium altissimum*, and *Asclepias syriaca* (forb species) (Foster et al., 2009).

The grassland management experiment was established in March 2000 (Figure 2; *see* Foster et al., 2009), consisting of a 4 × 4 grid containing 16 10 × 20 m plots, with 3 m buffer strips separating adjacent plots. Each 10 × 20 m plot was split into two 10 × 10 m subplots, creating 32 total subplots. Under this split-plot design, factorial treatments were applied at both the main-plot and subplot level. Two levels of nutrient fertilization (fertilized *vs* non-fertilized) and two levels of native prairie seed sowing (sown *vs* non-sown) were applied at the main plot level as between-subjects factors, and two levels of haying (hayed *vs* unhayed) were applied at the subplot level as a split-plot factor, thus creating four replicates of each treatment combination.

For the nutrient fertilization treatment, NPK (29-3-4) fertilizer was applied by hand to eight of the sixteen 10 × 20 m plots at a rate of 14-16 gN $m^{-2}yr^{-1}$. In most years (2003-2011), fertilizer was applied once in mid-April, but in 2001-2002, fertilizer was applied in two doses (8 gN m^{-2} in early April; 8 gN m^{-2} in late May/early June). For the haying treatment, one 10 × 10 m subplot in each 10 × 20 m plot was

hayed annually in mid-late June from 2002 to 2006. Haying during this period was conducted in June to coincide with typical cool-season hay management for the region. After 2006 haying management of the plots was altered to account for divergence in vegetation composition between fertilized and non-fertilized plots. By 2006 non-fertilized plots had become dominated by C_4 grasses which peak in biomass later in the summer than the C_3 hay grasses. A decision was made to continue haying the C_3-dominated fertilized plots in June, but to hay non-fertilized plots later in the summer as is typical for native hay meadows in the region that are dominated by C_4 grasses. After two years of rest, fertilized subplots were hayed in mid-June 2009 and non-fertilized subplots were hayed in early September 2009. Fertilized subplots were hayed again in mid-June 2010, but poor weather in July prevented haying of non-fertilized subplots in 2010. No subplots were hayed in 2011, the year of data collection for this study. As the latency since last haying differed between fertilized and non-fertilized plots, we interpret effects of haying with this discrepancy in mind. All subplots were not hayed for at least one year prior to the current study; therefore, we examine the long-term, cumulative effects of haying (*e.g.* reduced plant litter/habitat complexity, altered plant species composition) on arthropod community structure rather than immediate effects of haying (*e.g.* destruction of live plant material and vegetation-dwelling arthropods). For the sowing treatment, seeds of 41 native prairie species were sown by hand in eight of the sixteen 10 × 20 m plots in February 2003 and 2004 at a rate of 47 seeds/species/m^2. The species were selected due to their ubiquity in prairie hay meadows and natural occurrence in a nearby remnant prairie (Foster et al., 2009). The sowing mixture included prairie grasses, legumes, and non-legume forbs common to this region (Appendix A).

Vegetation sampling:

Vegetation in each 10 × 10 m subplot was surveyed from 2001 to 2011, but here we focus solely on data collected in 2011 and, thus, the surveying methods employed that year. We conducted plant cover surveys using a nested sampling design. We positioned three 1 m^2 sampling quadrats in three of the four subplot corners, separating the sampling quadrat from plot edges with a 2 m buffer. Within each quadrat,

we identified the plant species present and visually estimated each species' percentage cover. We combined species lists from the three quadrats and averaged species cover values to form a representative measure of each subplot's species composition. Cool-season (C_3) grasses typically reach peak abundance early in the growing season, whereas warm-season (C_4) grasses peak later in the season. Therefore we conducted cover surveys in all subplots between 1-13 June (when C_3 grasses were at peak abundance) and again in non-fertilized subplots where C_4 grasses dominate (Foster et al., 2009) between 14-21 July (when C_4 grasses were at peak abundance). We then averaged cover values among non-fertilized subplots across sampling dates, thus forming an integrative measure of plant community composition and abundance across the growing season.

To estimate plant productivity, we sampled aboveground standing crop biomass in all subplots between 24-31 May and non-fertilized subplots again between 11-12 July, again to best estimate and integrate peak production of C_3 and C_4 plant species. Using electric clippers, we harvested two 2 × 0.08 m strips of aboveground plant material per subplot and later sorted collected material to live and litter fractions. Both fractions were dried to constant mass at 74°C in a forced-air oven, then weighed. As non-fertilized subplots were sampled twice (in both May and July), we selected the biomass value for the date with peak abundance as each subplot's representative productivity. As fertilized plots were only sampled once, we simply used the biomass values for fertilized plots harvested in May.

Arthropod sampling

Arthropod surveys were conducted in each subplot using three collection methods: sweep-netting, pan-trapping, and pitfall-trapping. We chose these methods to sample the breadth of the arthropod community, including ground-dwelling (via pitfall traps), vegetation-dwelling (via sweep-netting), and aerial (via pan traps) arthropods. Sweep-netting was conducted on 13 June and 2 August 2011 in full sun at ~90°F. Each subplot was diagonally transected twice, and swept with a 0.38 m diameter canvas sweep net at approximately 1.5 m width × 1 m height. Sweeping was performed by one individual (M. Pesek) to standardize collection methods. Pitfall trapping was conducted overnight between 13-14 June and again

between 1-2 August 2011. We triangularly positioned three pitfall traps in each subplot, with 4 m between traps and a 2 m buffer from subplot edge. To set a pitfall trap, we positioned a plastic cup (266 ml) belowground with cup edge flush with the soil surface, and filled the cup with water and a small amount of soap to break surface tension. Pan trapping was conducted on 14 June and 1 August 2011. In early morning, we triangularly positioned three yellow plastic bowls (550 ml) on the soil surface within the vegetation, opposite of pitfall trap orientation, with 4 m between pan traps and 2 m buffers from subplot edge. Bowls were filled with water and a small amount of soap, and arthropods were collected from traps in mid-afternoon. All collected arthropods were stored in plastic freezer bags and frozen. Specimens were later identified and enumerated by one person (M. Pesek) to family level using print resources (McGavin, 2002; Salsbury, 2000; Ubick, 2005), with few enigmatic specimens identified to order or classified as unknown. Specimens were deposited at the Kansas Biological Survey and vouchers in the University of Kansas Entomology collections. We hereafter refer to arthropods classified to these taxonomic levels as OTUs (operational taxonomic units). To acquire integrative measures of arthropod OTU richness, evenness, Shannon's diversity, and abundance (number of individuals per subplot), we pooled species lists and summed abundances across collection methods for each subplot, then pooled species lists and averaged abundances across collection dates for each subplot.

Data analysis

Plant community responses:

We first evaluated plant community responses to our treatment regime, then used these responses as a predictive base from which to test effects of altered resources on consumer community structure, independent of experimental treatments. We constructed a blocked, split-plot analysis of variance (ANOVA), with fertilization and sowing as between-subjects factors and haying as a within-subjects factor. Plant responses included plant species richness, evenness, Shannon's diversity, and aboveground biomass (separated into 'live' and 'litter'). We used a log-transformation to homogenize variance for species richness.

To acquire an integrative measure of plant community response under our treatment regime, we tested for differences in plant species composition by conducting a PERMANOVA using the function 'adonis' in the R package 'vegan' (Oksanen, 2012). We calculated Bray-Curtis dissimilarity values for every possible pair of sites in a community matrix of relative plant species abundances, then entered this dissimilarity matrix into a blocked, split-plot PERMANOVA model, with sowing and fertilization as between-subjects factors and haying as a within-subjects factor. We calculated *F*- and *p*-values using 10,000 permutations. To determine if significant differences detected by PERMANOVA represented differences in group centroids or in dispersion of points among groups (Anderson, 2001), we also conducted a permutational analysis of dispersion (Anderson, 2006). We tested each significant factor in the PERMANOVA model using the function 'betadisper' in the R package 'vegan' (Oksanen, 2012) to calculate the average distance of group members to the group centroid, then permuted model residuals using 'permutest' to create a null permutation distribution and derive an *F*-statistic. Again, we ran 10,000 permutations on a Bray-Curtis dissimilarity matrix.

Arthropod community responses:

Next, we tested responses of the arthropod community structure to grassland management regimes and related these responses to those observed at the plant community level. These comparisons attempt to identify the plant community components primarily driving arthropod community assembly and structure as well as the management regimes underlying these relationships. We constructed a split-plot ANOVA, again with fertilization and sowing as between-subjects factors and haying as a within-subjects factor. In our model, we evaluated arthropod OTU richness, Shannon's diversity, evenness, and abundance (number of individuals per subplot) as response factors. To obtain normally distributed data, we square-root transformed arthropod abundance, square-transformed evenness, and square-transformed diversity. Upon detection of a significant effect of fertilization on arthropod abundance, we rarified arthropod richness to account for potential sampling bias, which can occur if a greater number of individuals are sampled at some sites than others, thus increasing the likelihood of detecting additional

taxa and artificially increasing measured richness (Gotelli, 2010). We included rarified richness of the whole arthropod community as an additional response variable in our ANOVA model.

Next, we tested arthropod community response at the microhabitat level to gain insight into how specific arthropod guilds respond to grassland management regimes and shifts in plant community structure. We use collection method (*i.e.* pitfall trap, pan trap, and sweep-netting) as an estimate for sampling distinct arthropod microhabitats (*i.e.* substrate-dwelling, aerial, and vegetation-dwelling, respectively). We report effects of collection method in terms of the microhabitat sampled hereafter. We ran three additional ANOVA models with the same factors as listed above, one for arthropods collected from each microhabitat. We did not include rarefied richness as a response variable in these models, for we could not obtain rarefied richness for nested subsets of arthropods due to the low number of individuals (*e.g.* number of individuals per subplot = 3) collected in some subplots. Due to violation of normality assumptions, we conducted a nonparametric Kruskal-Wallis rank sum test to test the interaction of sowing × fertilization × haying on substrate-dweller richness, reporting the chi-square and *p*-values instead of ANOVA F- and *p*-values (Table II). To reduce heteroscedasticity and obtain normally distributed data, we log-transformed aerial arthropod abundance and vegetation-dweller abundance. To obtain normally distributed data, we square-transformed vegetation-dweller evenness and diversity, and square-root transformed substrate-dweller abundance.

To evaluate treatment effects on arthropod OTU composition, we conducted PERMANOVAs (Anderson, 2001; McArdle & Anderson, 2001), and permutational analyses of dispersion (PERMDISP Anderson, 2006). We constructed two sets of PERMANOVA and dispersion models. The first examined the effect of the treatment regime on the whole arthropod community (pooled at the subplot level) with a blocking factor, sowing and fertilization as between-subject factors, and haying as a within-subjects factor. The second model included the same model terms as the first and one additional within-subject factor, collection method, to specifically test for differential effects of sowing, fertilization, and haying on arthropod assemblages within different microhabitats. To construct PERMANOVAs, we used the function

'adonis' in the R package 'vegan' (Oksanen, 2012), and to conduct dispersion analyses, we used the function 'betadisper' in the R package 'vegan' (Oksanen, 2012). For both sets of analysis, we calculated Bray-Curtis dissimilarity values for every possible pair of sites in a community matrix of relative arthropod species abundances, then entered this dissimilarity matrix into a blocked, split-plot PERMANOVA or dispersion model (with the same factor assignments as described in the above ANOVA model) using 10,000 permutations to calculate *F*- and *p*-values.

Multivariate regression and variance partitioning:

We explored independent effects of plant community composition, plant diversity, treatment regime, plant productivity, plant litter density, and spatial processes (patterns of spatial aggregation) by approximating the amount of variation explained by each aforementioned explanatory variable for each measure of arthropod community structure (richness (unadjusted for all groups and rarefied for whole community only), evenness, diversity, abundance, and composition). We conducted a series of distance-based linear models and variance partitioning at two sampling scales: 1) the whole community level, to identify drivers of overall arthropod community structure (hereafter referred to as 'whole community'); and 2) for each collection method within each subplot, including i) arthropods collected in pan traps only, to determine drivers of aerial arthropod community structure, ii) for arthropods collected in pitfall traps only, to determine drivers of substrate-dweller community structure, and iii) for arthropods collected by sweep-netting, to determine drivers of vegetation-dweller community structure.

For each arthropod sample (whole community, aerial, substrate-dwelling, and vegetation-dwelling) and community response (unadjusted and rarefied richness, evenness, diversity, abundance, and composition), we constructed six suites of predictor variables. To create our 'spatial' predictor suite, we included a series of third-order polynomials of the *X* and *Y* spatial coordinates of each experimental subplot. This approach allows detection of both linear and complex (*e.g* patches, gaps) trends of spatial aggregation (Borcard, Legendre, & Drapeau, 1992). 'Plant composition' predictors consisted of coordinates of three non-metric multidimensional scaling (NMDS) ordination axes best representing plant

community composition; 'experimental treatment' predictors included all independent and interactive effects of fertilization, sowing, and haying; 'plant diversity' predictors consisted of plant community species richness and evenness; 'plant productivity' included live aboveground biomass ($g \cdot m^{-2}$) as a predictor; and 'plant litter' included litter aboveground biomass ($g \cdot m^{-2}$) as a predictor.

To prepare the response matrix of arthropod composition, we calculated Bray-Curtis dissimilarity values for each pair of sites within each arthropod sample; and for arthropod richness, evenness, diversity, and abundance, we entered the univariate response variable vector into the model. We reduced the number of variables in each predictor suite using stepwise AIC model selection, with the function 'stepAIC' in the R package 'MASS' (Venables, 2002). We then conducted a dbRDA for each predictor suite (*e.g.* 'spatial', 'plant composition') using its reduced list of variables obtained through AIC, and further reduced our model by retaining only significantly predictive variables for each suite. At this point, if more than four suites contained significant predictor variables, we conducted a second stepwise AIC model selection and dbRDA to eliminate non-significant predictor suites and reduce the final number of predictive suites to four (or fewer) for variance partitioning.

We entered remaining predictive suites containing only significant terms into a model using the 'varpart' function in the R package 'vegan' (Oksanen, 2012) to determine the variation in arthropod community composition explained by each suite independent of other included suites, in addition to variation shared among suites and unexplained variance. We tested the significance of each included predictive suite by running RDA on each suite while controlling for effects of other predictive suites. See Table III for list of all potential variables and variables retained in final model for each arthropod sample and each response variable. For significant predictive suites of arthropod composition containing categorical variables (*i.e.* experimental treatment predictors), we ran the function 'simper' in the R package, 'vegan' (Oksanen, 2012), which finds the average contributions of OTUs to each groups' overall dissimilarity by performing pairwise comparisons among groups and identifying characterizing taxa (list of variables tested in 'simper' in Table III).

RESULTS:

Plant community structure and productivity

Fertilization significantly reduced plant species richness, evenness, and Shannon diversity, but to a lesser extent in hayed plots (fertilization × haying interactions: Table I, Fig 3). Haying increased plant species richness in fertilized plots only. Haying decreased species evenness and diversity in non-fertilized plots, but increased evenness and diversity in fertilized plots. Sowing increased all measures of diversity, although in the case of Shannon diversity – and marginally so for species richness – this effect was greater in non-fertilized plots (fertilization × sowing interaction: Table I, Fig 3). Fertilization tended to increase live biomass (Table I, Fig 3); and haying reduced litter biomass in fertilized plots only (fertilization × haying interaction: Table I, Fig 3).

Plant communities sown with native seeds harbored species assemblages distinct from those not sown (sowing effect: $F = 4.910$, $p = 0.010$; Fig 4), an effect more pronounced in non-fertilized plots (sowing × fertilization interaction: $F = 0.460$, $p = 0.011$; Fig 4). Among non-sown – but not sown – plots, fertilization reduced compositionally variability (sowing × fertilization effect on dispersion: $F = 4.3636$, $p = 0.0106$). Plant species assemblages in fertilized plots had centroids distinct from those in non-fertilized plots (fertilization effect: $F = 39.625$, $p < 0.001$; Fig 4), and assemblages in fertilized plots were less variable than those in non-fertilized plots (fertilization effect on dispersion: $F = 37.968$, $p < 0.001$). Assemblages in hayed subplots were compositionally distinct from those in unhayed subplots (haying effect: $F = 3.7889$, $p = 0.006$; Fig 4). Plant species assemblages in non-fertilized plots experienced a greater shift in composition in response to haying than those in fertilized plots (fertilization × haying interaction: $F = 25.8519$, $p < 0.001$; Fig 4), and non-fertilized plots increased in compositional variability in response to haying, whereas fertilized plots did not (fertilization × haying interaction on dispersion: $F = 19.844$, $p < 0.001$).

Arthropod abundance and diversity

Overall, arthropods were more abundant in non-fertilized plots than in fertilized plots (fertilization effect: Table II, Fig 5); this main effect was consistent among aerial arthropods only (fertilization effect: Table II, Fig 5). Vegetation-dweller abundance was driven by an interaction between fertilization and haying; haying strongly reduced vegetation-dweller abundance in non-fertilized plots only (fertilization × haying interaction: Table II, Fig 5). Substrate-dweller abundance was not affected by experimental treatments.

At the whole community level, haying reduced arthropod (unadjusted) richness (haying effect: Table II, Fig 5). Upon rarefaction, fertilization alone mediated richness; rarefied richness was greater in fertilized than non-fertilized plots (fertilization effect: $F = 5.093$, $p = 0.0435$), which suggests that arthropod richness is contingent on arthropod abundance. While we do not graphically display responses of rarefied richness or analyze rarefied richness within nested arthropod assemblages, we consider this contingency when further analyzing and interpreting whole arthropod richness responses. Drivers of arthropod richness varied greatly according to microhabitat. Fertilization tended to decrease aerial arthropod richness (fertilization effect: Table II, Fig 5); and haying decreased aerial richness only in non-fertilized plots (fertilization × haying interaction: Table II, Fig 5). Haying decreased vegetation-dweller richness in non-fertilized plots only (fertilization × haying interaction: Table II, Fig 5). Responses of substrate-dweller richness were complex; sowing increased substrate-dweller richness except in plots that were both non-fertilized and unhayed (sowing × haying × fertilization interaction: Table II, Fig 5).

Fertilization increased whole arthropod community evenness (fertilization effect: Table II, Fig 5) and, similarly, increased aerial arthropod evenness (fertilization effect: Table II, Fig 5). Haying reduced vegetation-dweller evenness in non-fertilized plots but had no effect in fertilized plots (fertilization × haying interaction: Table II, Fig 5); and substrate-dweller evenness was unaffected by experimental factors. Fertilization significantly increased vegetation-dweller diversity (fertilization effect: Table II, Fig

5), but had no effect on whole community, aerial, and substrate-dwelling arthropod diversity (Table II, Fig 5).

Arthropod species composition

Overall, arthropod assemblages in fertilized plots were compositionally distinct from those in non-fertilized plots (fertilization effect: $F = 9.4099$, $p = 0.0002$; Fig 6), and, to a lesser extent, hayed subplots held assemblages distinct from those in unhayed subplots (haying effect: $F = 1.8677$, $p = 0.0239$; Fig 6). Haying caused a greater shift in arthropod OTU composition in fertilized plots than those in non-fertilized plots (fertilization × haying interaction: $F = 5.4801$, $p = 0.0252$; Fig 6). Differences in arthropod community composition across treatment levels were due solely to differences between group centroids, not point dispersions (dispersion effects – fertilization effect: $F = 3.2341$, $p = 0.07259$; haying effect: $F = 0.0121$, $p = 0.9101$; fertilization × haying interaction: $F = 0.6483$, $p = 0.593$).

Arthropod assemblages sampled from different microhabitats differed in OTU composition ($F = 56.821$, $p < 0.0001$; Fig 7) as well as in compositional variability ($F = 14.564$, $p < 0.001$), with aerial arthropod assemblages more variable than both substrate-dwelling assemblages ($p < 0.0001$) and vegetation-dwelling assemblages ($p = 0.0478$), and vegetation-dwelling assemblages more variable than substrate-dwelling assemblages ($p = 0.01491$). Vegetation-dweller composition experienced the greatest shift in composition in response to fertilization, followed by substrate-dweller composition (which experienced a lesser shift), and aerial arthropod composition (which did not appear to shift in composition) (microhabitat × fertilization interaction: $F = 6.539$, $p < 0.0001$; Fig 7). Changes in compositional variability with fertilization level varied among microhabitats; with fertilization, vegetation-dwelling arthropod assemblage variability decreased the most, followed by substrate-dwelling and aerial arthropod variability, respectively (microhabitat × fertilization interaction: $F = 8.5312$, $p < 0.0001$; Fig 7).

Multivariate regression and variance partitioning of arthropod community structure

At the whole community level, unadjusted arthropod richness was predicted most by plant species evenness (r = 0.3633) and litter biomass (r = 0.4525) (Table IV), whereas rarefied richness was significantly predicted by spatial effects (F = 7.9567, p = 0.005) and plant species composition (F = 19.703, p = 0.005). Aerial arthropod richness was significantly predicted by plant species evenness (r = 0.4287; Table IV). However, vegetation-dweller richness and substrate-dweller richness were not significantly explained by any predictor suites, and nearly all variation was left explained for both arthropod groups (Table IV).

Spatial predictors and plant species composition explained significant amounts of variation in whole community evenness and diversity. Similarly, variation in aerial and substrate-dweller evenness was significantly explained by spatial predictors; and variation in vegetation-dweller evenness and diversity was significantly explained by plant species composition (Table IV). Aerial arthropod diversity and substrate-dweller diversity were not predicted by any variables, leaving (respectively) 100% and 94% of variation unexplained.

Whole community arthropod abundance was predicted by spatial variables and fertilization regime (with higher abundances found in non-fertilized plots), and aerial arthropod abundance was best predicted by plant species composition (Table IV). Substrate-dweller abundance was significantly predicted by both spatial variables and plant species composition (Table IV). No variables significantly predicted vegetation-dweller abundance, leaving 84% of variation unexplained.

At the whole community level, arthropod composition was primarily predicted by spatial effects, followed by effects of plant community composition (Table IV). Variation in substrate-dweller composition was highly predicted both by spatial variables and plant diversity (Table IV). While no significant predictors for aerial arthropod composition were found (leaving 97% of variation unexplained), composition of vegetation-dwellers was best explained by fertilization and haying regimes (Table IV). As found by simper analysis, vegetation-dweller composition in fertilized plots was typified

by black flies, orb-weaving spiders, leafhoppers, and katydids (Orthoptera: Tettigoniidae); while vegetation-dweller composition in non-fertilized plots was typified by jumping plant lice, leaf beetles, and jumping spiders (Araneae: Salticidae). Hayed subplots were characterized by black flies, jumping spiders, leafhoppers, orb-weaving spiders, katydids, and lynx spiders; and unhayed subplots were characterized by jumping plant lice and leaf beetles.

DISCUSSION:

Here, we demonstrate that different grassland management regimes and associated effects on plant community structure influence arthropod community structure. We investigate arthropod responses at two levels: the whole community level (experiment subplots) and within three microhabitats nested within each whole community, which contain compositionally distinct assemblages (effect of collection method on arthropod composition: Fig 7). For the whole arthropod community, we find limited support for the RDH, PLH, and PCH; likely due to disparate responses of different arthropod groups nested within whole communities. Also, we find some support for the RDH among aerial and substrate-dwelling arthropods; the DEM among aerial arthropods; and the PCH among aerial, vegetation-dwelling, and substrate-dwelling arthropods. Spatial processes independent of local resources significantly affect several components of consumer community structure at both the whole community scale and within nested microhabitats. Our findings demonstrate the value of investigating patterns at multiple spatial scales (whole and nested communities) and of evaluating the relative influences of local resources versus spatial processes to determine general and niche-specific drivers of consumer community structure.

Effects of resource diversity

Both observational (Kirchner, 1977; Southwood et al., 1979) and empirical (Haddad et al., 2009; Haddad, Haarstad, & Tilman, 2000; Perner et al., 2003; Siemann et al., 1998) studies have provided evidence for positive relationships between plant diversity and diversity of higher trophic levels, *i.e.* the RDH; and we expect to observe similar relationships between plant and arthropod communities in our

study system. As predicted by the RDH, plant species evenness positively affects whole community arthropod (unadjusted) richness and is associated with substrate-dweller composition (variance partitioning, see Table IV). However, the relationship between plant species evenness and whole arthropod richness is lost upon rarefaction and appears to be caused by a sampling effect, *i.e.* the number of arthropod individuals is greater in non-fertilized than fertilized plots (Fig 5). Increased plant diversity has been seen to increase arthropod abundance and, consequently, arthropod richness in other systems (Haddad et al., 2009; Srivastava & Lawton, 1998), possibly due to greater structural complexity, available resource types, and/or shared phylogenetic history associated with diverse plant communities. Here, increased equitability of plants species – and resource types – in the absence of fertilization may promote the abundance of consumer taxa with preferences or specializations to these plant species/resources types. Non-fertilized plots contain plant communities in which species and functional guilds are more equitably represented by a variety of C_3 forbs, cool-season grasses, and native, warm-season C_4 grasses in comparison to fertilized plots, which are dominated by 2-3 highly productive C_3 grasses. The more equitable representations of these plant species in non-fertilized plots may allow consumers greater opportunity for specialization on functionally diverse resources that are, generally, not rare and not at risk of extinction. Thus, more equitable representations of plant species and functional guilds may create a greater number of stable opportunities for niche specialization and coexistence among consumers (Siemann et al., 1998), as found here.

Plant diversity and productivity respond to fertilization and disturbance regimes as predicted by the DEM (Fig 3), allowing us to test the extent to which models predicting plant diversity can predict diversity at higher trophic levels. Fertilization does not affect unadjusted whole arthropod richness and diversity and, surprisingly, increases rarefied arthropod richness and whole community evenness – trending in the direction opposite of which we expected (Fig 5). Fertilization decreases aerial arthropod richness, as predicted by the DEM, but haying fails to increase aerial arthropod richness in fertilized plots as it did for plants (Fig 5). Overall, aerial arthropod richness alone shows patterns consistent with some

aspects of the DEM. Strong positive links between plant and aerial arthropod richness may be due to the high proportion of pollinating taxa constituting this assemblage, which contains nectivorous taxa from Diptera, Hymenoptera, and Coleoptera. Pollinator diversity has been found to share a positive relationship with floral diversity (Frund, Linsenmair, & Bluthgen, 2010), which is determined by plant species composition and diversity. At our study site, fertilization causes a divergence in plant species diversity and species composition, and likely influences floral diversity; low-diversity, fertilized plots contain mostly wind-dispersing grass species, while high-diversity, non-fertilized plots contain a variety of insect-pollinated prairie forbs, including Canada goldenrod (*Solidago canadensis*), prairie sage (*Salvia azurea*), and roundhead bushclover (*Lespedeza capitata*). The increased availability of pollinator niches in high diversity, non-fertilized plots may be promoting aerial arthropod richness here. Additionally, a higher diversity of pollinating arthropods and higher rates of pollination in non-fertilized plots may create positive feedbacks to the plant community, increasing the reproductive fitness and abundance of biotically pollinated plant species, *i.e.* prairie forbs.

To control for confounding effects of productivity while further testing the RDH, we experimentally sow seeds of prairie plant species, thus increasing plant species diversity independent of site productivity in non-fertilized plots (Fig 3). In non-fertilized plots, seed addition affects neither whole arthropod diversity nor diversity of either aerial or vegetation-dwelling arthropods (Table II; Fig 5); but does increase richness of substrate-dwellers in fertilized, hayed plots (Fig 5). However, variance partitioning reveals no effect of plant diversity on substrate-dweller richness or diversity (Table IV). The absence of strong plant-arthropod diversity relationships here in addition to limited support for the DEM may reflect dampening of positive resource diversity effects via top-down pressures of predation/parasitism or alterations to the pathway (direct *vs* indirect) of resource diversity effects via trophic interactions (Haddad et al., 2009; Haddad et al., 2000; Siemann, 1998; Siemann et al., 1998). Many studies have identified dampened effects of plant diversity when examining patterns within and across trophic guilds due to guild-specific responses (Haddad et al., 2009; Haddad et al., 2000; Hartley &

Jones, 2003; Perner et al., 2003; Siemann, 1998; Siemann et al., 1998). Guild-specific responses may be similarly dampening relationships between plant and arthropod diversity here, although we do not explore this possibility in this study. Instead, we identify disparate responses to altered plant diversity (Fig 5) among spatially separated, compositionally distinct assemblages (Fig 7) – each of which may forage or utilize habitat differently. For example, spatially distinct taxa may utilize different trophic niches (*e.g.* substrate-dwellers may constitute a large number of detritivores; many aerial arthropods may be pollinators) or, within each trophic guild, taxa may differ in their feeding behaviors and specializations (*e.g.* vegetation-dwelling herbivores may consume leaf tissue; substrate-dwelling herbivores may consume root or stem tissue). Further work is needed to elucidate and separate plant-arthropod diversity relationships specific to both trophic guilds and microhabitats.

Effects of resource abundance

Fertilization tends to increase plant productivity while concomitantly reducing plant diversity (Fig 3); thus, we can test the RAH to examine how augmented productivity despite simultaneous declines in plant diversity affects consumer abundance and diversity. While fertilization significantly increases whole community rarefied richness, Shannon diversity of vegetation-dwelling arthropods, and whole community and aerial arthropod evenness (Fig 5), plant productivity does not share a significant relationship with diversity and/or abundance of any arthropod assemblage (Table IV). Instead, arthropod abundance and diversity share stronger relationships with plant species composition, spatial effects, and/or treatment effects than with productivity (Table IV); thus, the RAH does not appear to be determining consumer diversity or abundance. Resource abundance is generally hypothesized to positively affect consumer abundance and – consequently – diversity (Abrams, 1995; Srivastava & Lawton, 1998). Results from Siemann (1998) support this hypothesis, with increased productivity supporting more abundant and diverse arthropod assemblages. Clearly, these results differ from ours, which is likely due to differences in experiment design: Siemann independently augmented productivity without altering plant diversity, whereas we do not. Any potential positive effects of increased

productivity on arthropod abundance and diversity here may have been cancelled out by concurrent negative effects of reduced plant diversity equal or greater in effect size. This possibility is likely, for we detect a positive relationship between plant and arthropod diversity and link this relationship to a sampling effect (Table IV).

Effects of plant litter

In support of the plant litter hypothesis (PLH), whole arthropod community richness is positively related to plant litter biomass (Table IV), possible due to increased architectural complexity (Lawton, 1983; Rypstra et al., 1999), mollification of harsh abiotic conditions (Facelli & Pickett, 1991), and/or increased abundance of resources available to detritivores (Wardle et al., 2006). However, experimental manipulations to litter biomass via haying (Fig 3) do not affect arthropod richness (Fig 5), and, unexpectedly, haying reduces aerial and vegetation-dwelling arthropod richness in non-fertilized plots. As opposed to changing the abiotic environment, litter removal via haying may alter plant species composition and thus affect aerial and vegetation-dwelling arthropods. Non-fertilized, hayed plots contain mostly C_4 graminoid species, while non-fertilized, unhayed sites contain a diverse mix of C_3 grasses and forbs and C_4 grasses. Lower nutritional value and palatability of C_4 plants in comparison to C_3 (Caswell et al., 1973) may encourage preferential feeding by herbivores, and could in turn lead to aggregations of herbivorous species (Wardle et al., 1999) and their respective predators and parasites in diverse, C_3 species-rich habitats (non-fertilized, unhayed sites), which may tie to adverse haying effects in non-fertilized plots seen here.

Effects of plant species composition

Many consumer taxa are known to specialize on one or few closely related host species (Bernays & Graham, 1988); thus, shifting the identity and abundance of plant species may induce corresponding shifts in consumer composition and regulate other components of consumer community structure, *e.g.* richness, abundance, *etc*. In support of the PCH, shifts in arthropod composition in response to experimental treatments (Fig 6) generally parallel shifts in plant composition (Fig 4), and several

components of community structure in different consumer assemblages are strongly influenced by plant species composition (Table IV; whole rarefied richness). These patterns agree with past studies, which have found plant species and functional group composition to explain the greatest amount of variation in arthropod composition (Schaffers et al., 2008; Symstad, Siemann, & Haarstad, 2000) and abundance (Koricheva et al., 2000) relative to traditional metrics of plant diversity, vegetation structure, and local environmental factors. As argued by Schaffers *et al* (2008), strong effects of plant species composition does not imply that this measure is more influential than traditional metrics of plant diversity and vegetation structure *per se*, but that plant composition may emerge as the best predictor of arthropod community structure due to 1) direct effects of plant species/host identity on specialist consumers, and 2) the integration of resource diversity, structure, and the local environment into one multi-faceted measure. Many responses of the arthropod community are linked to plant species composition here, likely due to both direct effects and the integrative nature of plant species composition.

Effects of spatial processes

Several components of whole and substrate-dweller community structure, in addition to aerial arthropod evenness, are related to spatial patterns. Spatial structure found among vagile taxa within the whole community and aerial assemblages (Table IV) may be caused by mass and/or rescue effects, in which rare or diminishing taxa are sustained in sink sites by flow of individuals from more densely populated sites (Leibold et al., 2004; Mouquet & Loreau, 2003) and are relatively unaffected by local environmental conditions within habitat patches. However, here we find plant species evenness and richness to be related to whole arthropod richness and aerial richness, respectively. These relationships suggest that, while these vagile taxa are probably dispersing across this matrix of habitat patches, they are also influenced by local resource conditions. Dependency on both local factors and dispersal is consistent with the species-sorting paradigm of metacommunity ecology (Leibold et al., 2004), which suggests that assemblages assemble and continuously sort along environmental gradients but are also influenced by dispersal across habitat patches.

In particular, substrate-dwellers exhibit high spatial organization, which may be related to the relatively low vagility of taxa in this group (Jeanneret et al., 2003). Substrate-dweller assemblages consist mainly of epigeal taxa (woodlice, ants, wolf spiders, and carabid beetles) that are comparatively less vagile than winged insects (Orthoptera, Hemiptera, Diptera) and wind-dispersing spiders (Araneae: Oxyopidae, Araneidae) common to other microhabitats. Low rates of dispersal among habitat patches can result in increased importance of local environmental conditions on local species interactions and diversity (Leibold et al., 2004), which may explain the higher-order spatial aggregations of substrate-dweller evenness, abundance, and composition detected here (Table III, IV).

Direct effects of experimental treatments

Direct effects of fertilization and haying significantly affect vegetation-dweller composition, and fertilization negatively affects whole community abundance (Table IV), indicating that effects independent from associated shifts in plant diversity, productivity, and composition are at work. Changes to plant tissue nitrogen and/or chemical properties of the local environment (*e.g.* pH) may underlie direct effects of fertilization, while changes to habitat structure independent of plant litter density may underlie direct effects of haying. Alternatively, direct effects of haying may be due to discrepancies in time since last haying; however, as fertilization and haying do not interact to cause stronger effects in fertilized plots (which were more recently hayed), this explanation is unlikely. Overall, reasons underlying direct effects of treatment regimes are difficult to infer here, and require further investigation.

Conclusion

In summary, we find several sources of variation to drive primary (herbivore) and secondary consumer structure – including characteristics of the plant community, direct effects of grassland management, and spatial processes – yet the strengths of these effects are highly variable and are often niche-specific (*i.e.* dependent on microhabitat). We find the most evidence for the PCH (plant species composition) and control by spatial processes in shaping arthropod diversity, abundance, and composition; and weaker support for effects of resource diversity (RDH and DEM) and plant litter (PLH).

Despite support for several hypotheses, much variation is left unexplained (Table IV), likely due to the high complexity of consumer communities, *e.g.* diversity of trophic levels represented and niche-specific pressures of predation, competition, and abiotic stress. As demonstrated by our study, consumer communities assemble – in part – in response to resource structure and spatial processes, yet are likely driven by other unidentified factors, one of which may be opposing or dampening responses among different trophic guilds (Haddad et al., 2009; Haddad et al., 2000; Siemann, 1998; Siemann et al., 1998; Symstad et al., 2000). The complexity of community responses – and variability of guild-specific responses – should be considered when managing or restoring TGP ecosystems and the consumer communities within.

TABLES AND FIGURES:

Table I: Sources of variation in plant community structure. Sources of variation include the between-subjects factors *Fert* (Fertilization) and *Sow*, and the within-subjects factor, *Hay*. Significance is labeled as follows: •$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

		Species richness		Evenness		Shannon diversity index		Live biomass		Litter biomass	
Source	d.f.	MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Within-subjects effects											
Hay	1	1.6136	25.621***	0.03899	3.505•	0.0610	1.283	5172	1.706	227538	8.835*
Hay × Fert	1	1.3129	20.8470***	0.15722	14.135**	2.6848	56.492***	6193	2.043	180544	7.010*
Hay × Sow	1	0.0295	0.469	0.00347	0.312	0.0873	1.836	1855	0.612	42341	1.644
Hay × Fert × Sow	1	0.0787	1.249	0.01033	0.929	0.0037	0.077	4238	1.398	11128	0.432
Error(Hay)	12	0.0630		0.01112		0.0475		3032		25754	
Between-subjects effects											
Fert	1	10.232	166.012***	0.28407	28.398***	9.037	109.092***	38239	4.644•	44118	1.614
Sow	1	0.724	11.740**	0.19205	19.198***	3.036	36.655***	636	0.077	25379	0.929
Fert × Sow	1	0.257	4.175•	0.00984	0.983	0.710	8.566*	217	0.026	11918	0.436
Error	12	0.062		0.01000		0.083		8234		27327	

• $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table II: Sources of variation in arthropod community structure, with communities for each arthropod sample (whole community and aerial, vegetation-dwelling, and substrate-dwelling arthropods). Sources of variation include the between-subjects factors *Fert* (Fertilization) and *Sow*, and the within-subjects factor, *Hay*. Significance is labeled as follows: •$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. † denotes use of Kruskal-Wallis rank sum test and reports a χ^2 statistic.

			Species richness		Evenness		Shannon diversity index		Abundance	
Sample	Source	*df*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Whole community	Within-subjects effects									
	Hay	1	128.00	19.08***	0.03	1.26	0.06	0.03	6.15	1.51
	Hay × Fert	1	24.50	3.65•	0.03	1.70	4.01	2.17	2.11	0.52
	Hay × Sow	1	0.50	0.08	0.01	0.30	0.54	0.29	4.15	1.02
	Hay × Fert × Sow	1	0.50	0.08	0.01	0.46	0.97	0.52	5.56	1.37
	Error(Hay)	12	6.71		0.02		1.85		4.06	
	Between-subjects effects									
	Fert	1	8.00	0.88	0.32	5.73*	25.10	4.46•	67.46	6.40*
	Sow	1	12.50	1.37	0.00	0.01	0.64	0.11	0.16	0.02
	Fert × Sow	1	0.00	0.00	0.00	0.06	0.17	0.03	0.33	0.03
	Error	12	9.13		0.06		5.62		10.54	
Aerial arthropods	Within-subjects effects									
	Hay	1	3.78	1.46	0.013	0.65	0.15	1.38	0.01	0.04
	Hay × Fert	1	13.78	5.31*	0.006	0.29	0.26	2.37	0.05	0.23
	Hay × Sow	1	5.28	2.04	0.00	0.00	0.08	0.73	0.04	0.18
	Hay × Fert × Sow	1	2.53	0.98	0.00	0.00	0.03	0.24	0.03	0.12
	Error(Hay)	12	2.59		0.02		0.11		0.24	
	Between-subjects effects									
	Fert	1	19.53	5.25*	0.13	6.72*	0.04	0.28	3.57	17.71**
	Sow	1	0.03	0.01	0.01	0.37	0.05	0.35	0.01	0.05
	Fert × Sow	1	0.28	0.08	0.01	0.75	0.07	0.49	0.00	0.02
	Error	12	3.72		0.02		0.15		0.20	
Vegetation-dwelling arthropods	Within-subjects effects									
	Hay	1	75.03	11.31**	0.27	17.93**	0.22	0.13	2.63	16.95**
	Hay × Fert	1	87.78	13.23**	0.32	20.89***	0.12	0.07	5.23	33.63***
	Hay × Sow	1	0.03	0.01	0.00	0.00	0.34	0.20	0.01	0.06
	Hay × Fert × Sow	1	9.03	1.36	0.01	0.59	3.70	2.18	0.00	0.02
	Error(Hay)	12	6.64		0.02		1.70		0.16	
	Between-subjects effects									
	Fert	1	9.03	1.08	0.12	9.97**	13.59	10.73**	0.00	0.00
	Sow	1	0.78	0.09	0.01	0.43	0.01	0.01	0.31	2.73
	Fert × Sow	1	5.28	0.63	0.03	2.31	0.01	0.01	0.13	1.10
	Error	12	8.34		0.01		1.27		0.11	
Substrate-dwelling arthropods	Within-subjects effects									
	Hay	1	0.50	0.15	0.01	0.55	0.02	0.34	0.58	0.14
	Hay × Fert	1	4.50	1.35	0.00	0.34	0.01	0.12	3.05	0.71
	Hay × Sow	1	12.50	3.74•	0.01	1.06	0.14	2.26	3.75	0.87
	Hay × Fert × Sow	1	N/A†	5.52*†	0.00	0.02	0.05	0.78	3.36	0.78
	Error(Hay)	12	3.35		0.01		0.06		4.31	
	Between-subjects effects									
	Fert	1	1.13	0.25	0.09	1.73	0.46	1.70	64.37	4.21•
	Sow	1	28.13	6.19*	0.00	0.09	0.24	0.89	2.14	0.14
	Fert × Sow	1	3.13	0.69	0.03	0.55	0.30	1.10	0.00	0.00
	Error	12	4.54		0.05		0.27		15.27	

Table III: Summary of variables – categorized by predictive suite and classified as either continuous ("cont") or categorical ("cat") – available to multivariate regression and variance partitioning for each sample ("W" – whole community; "A" – aerial arthropods; "V" – vegetation-dwelling arthropods; "S" – substrate-dwelling arthropods). For each predictive suite, variables were first run through AIC model selection and redundancy analysis, and significant terms were retained in final model (included terms denoted by '×'). Predictive suites containing these significant terms were included in final dbRDA and variation partitioning analyses. Variables included in simper analysis are marked with †. Arthropod samples with no significant predictors – variables and predictor suites – are denoted with *.

			Included in final model:																			
			Richness				**Evenness**				**Diversity**				**Abundance**				**Composition**			
Predictive Suite	*Variable*	*Type*	W	A	V	S*	W	A	V	S	W	A*	V	S	W	A	V	S	W	A	V	S
Spatial	x	cont		×			×			×	×			×						×		
	y	cont					×			×	×			×								
	x^2	cont								×	×			×								
	y^2	cont					×			×	×			×	×			×				
	x^3	cont																				
	y^3	cont						×							×			×	×			×
	xy	cont			×		×			×	×		×	×	×	×		×	×			×
	xy^2	cont			×		×			×	×		×	×	×	×		×	×			×
	x^2y	cont		×				×														
Plant Composition	NMDS1	cont					×	×		×	×		×		×	×	×	×	×	×	×	×
	NMDS2	cont																				
	NMDS3	cont							×													
Experimental Treatment	fertilization	cat						×			×				×	×		×	×		×†	×
	haying	cat																			×†	
	sowing	cat																				
	fert:hay	cat		×	×				×								×					
	fert:sow	cat																				
	sow:hay	cat																				
	fert:sow:hay	cat																				
Plant Diversity	richness	cont									×				×	×		×	×		×	×
	evenness	cont	×	×					×								×					
Productivity	live biomass	cont									×				×	×		×	×		×	×
Plant Litter	litter biomass	cont	×																			

Table IV. Summary of adjusted R^2 values for each predictive suite/residuals, obtained through variance partitioning for each sample (labeled as: "W" – whole community; "A" – aerial arthropods; "V" – vegetation-dwelling arthropods; "S" – substrate-dwelling arthropods). Adj. R^2 values of significant predictive suites are bolded and labeled as follows: *$p < 0.05$; **$p < 0.01$. Values for suites not included in final model are marked with "-".

		Predictive Suite							
Response		*Spatial*	*Composition*	*Treatment*	*Diversity*	*Productivity*	*Litter*	*Shared*	*Residuals*
Richness	W	-	-	-	**0.08410***	-	**0.15945***	0.01671	0.73973
	A	-0.01701	-	-0.02833	**0.16042***	-	-	-0.00479	0.88971
	V	0.01574	-	-0.03157	-	-	-	0.01118	1.00465
	S	-	-	-	-	-	-	-	-
Evenness	W	**0.30205****	**0.17243****	-	-	-	-	0.06507	0.46046
	A	**0.17228***	-0.00124	-0.02227	-	-	-	0.21823	0.63298
	V	-	**0.12100***	0.03977	0.0198	-	-	0.0804	0.73901
	S	**0.45661****	0.04233	-	-	-	-	0.05124	0.44982
Diversity	W	**0.38469****	**0.18730***	-	-	-	-	0.04452	0.38349
	A	-	-	-	-	-	-	-	-
	V	0.04067	**0.13340***	-	-	-	-	0.00750	0.81844
	S	0.05973	-	-	-	-	-	-	0.94027
Abundance	W	**0.36864****	-	**0.18832****	-	-	-	0.01731	0.42573
	A	0.03236	**0.28161****	-	-	-	-	-0.01734	0.70337
	V	-	0.07570	-0.02377	0.01992	-	-	0.09167	0.83648
	S	**0.35000****	**0.14004****	-	-	-	-	0.08137	0.42859
Composition	W	**0.14395****	**0.06232****	0.01684	-	-	-	0.24018	0.53670
	A	-0.00519	0.02820	-	-	-	-	0.00038	0.97660
	V	-	0.00788	**0.15738****	-0.00033	-0.01106	-	0.27838	0.56773
	S	**0.15424****	-	-	**0.24808****	-	-	0.07621	0.52148

Figure 1. Diagram outlining alternative hypotheses. The upper half of the diagram contains potential direct effects of plant diversity, productivity, disturbance, and composition on the consumer community, with solid arrows directly connecting the predictive factors with the expected outcome. The lower half tracks potential indirect, interactive effects of plant diversity, productivity, and disturbance on the consumer community, with dashed arrows first connecting the predictive factors to expected responses of plant diversity, and secondly to the corresponding expected consumer community response. Specific models or hypotheses underlying our expectations are printed in bold (RDH – resource diversity hypothesis; RAH – resource abundance hypothesis; PLH – plant litter hypothesis; PCH – plant composition hypothesis; DEM – Dynamic Equilibrium Model).

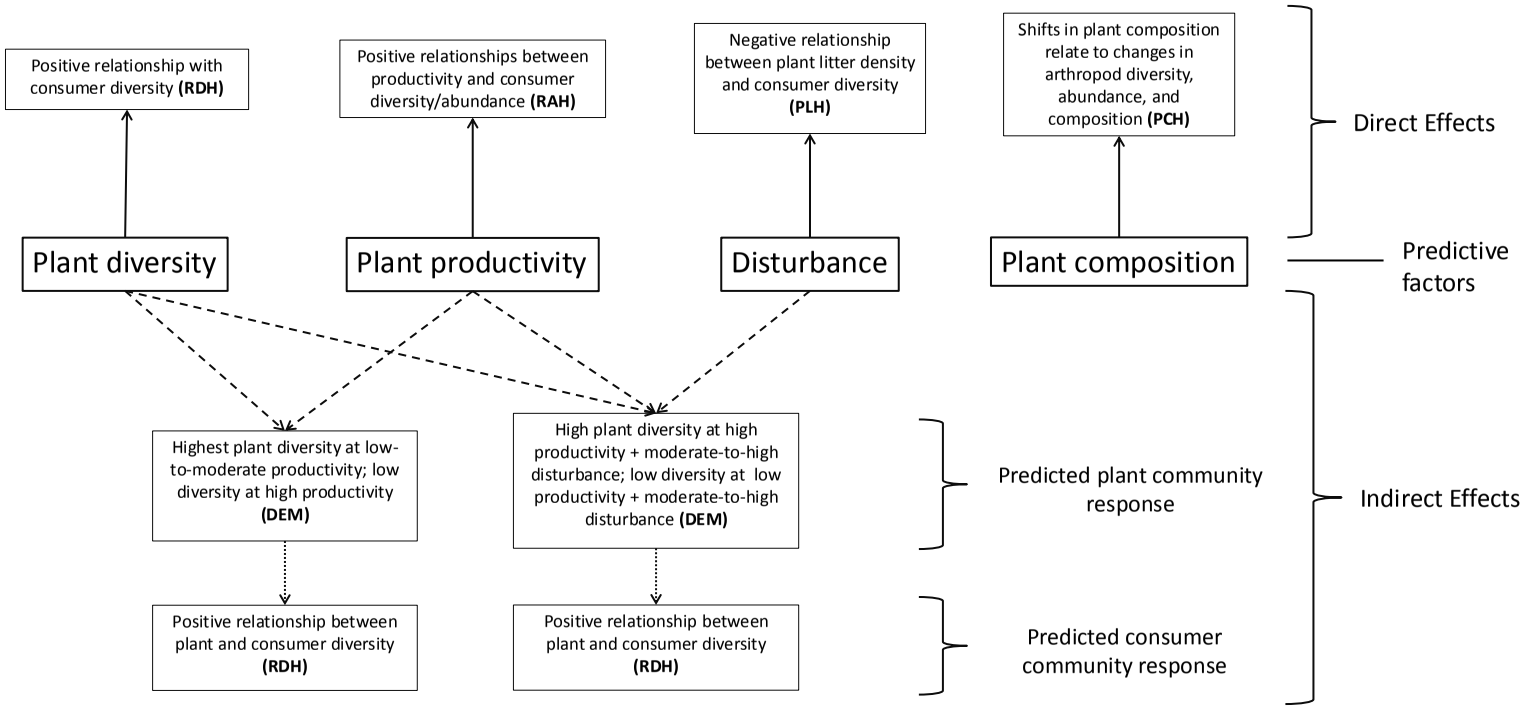


Figure 2. Experimental design of grassland management regimes. See legend for treatment designations (‘fert’ – fertilization level; ‘hay’ – haying level; ‘sow’ – sowing level).

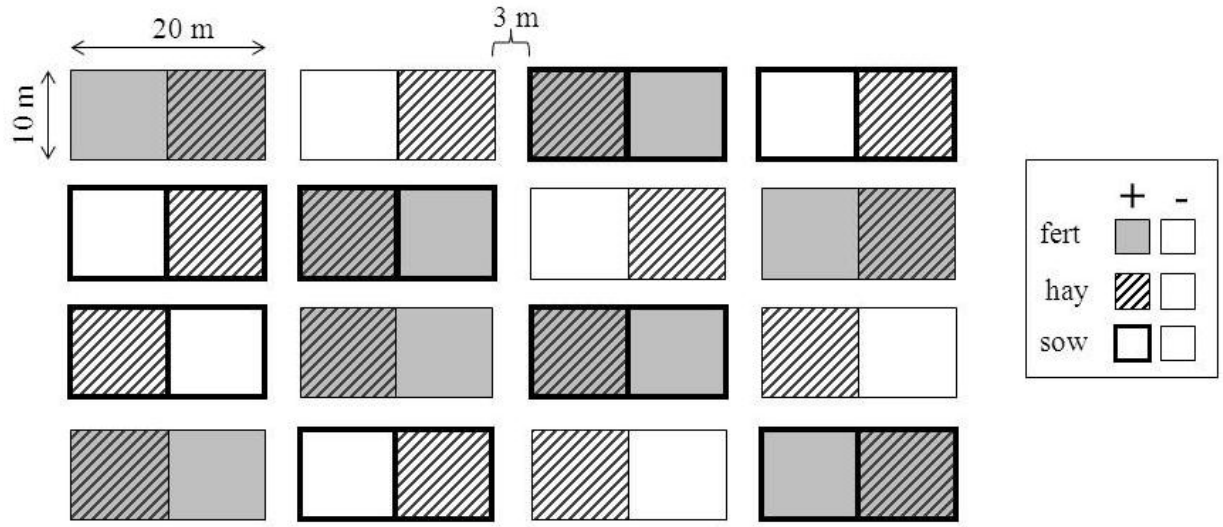


Figure 3. Responses of plant richness, evenness, diversity, and live/litter biomass to treatment effects. Richness, evenness, and diversity responses are shown on separate rows, and live and litter biomass are shown side-by-side on the bottom row. Significant effects and interactions are noted in upper left corner of each graph ("F" – fertilization effect; "H" – haying effect; "S" – sowing effect; "F×H" – fertilization by haying interaction; "F×S" – fertilization by sowing interaction; "ns" – no significant effects), and significance levels are included (•$p < 0.10$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.01$). Legends are abbreviated as follows: "NH"/"H": not hayed/hayed; "NF"/"F": not fertilized/fertilized; "NS"/"S": not sown/sown. Note different legends among panels and, for the bottom row, different y-axes between figures.

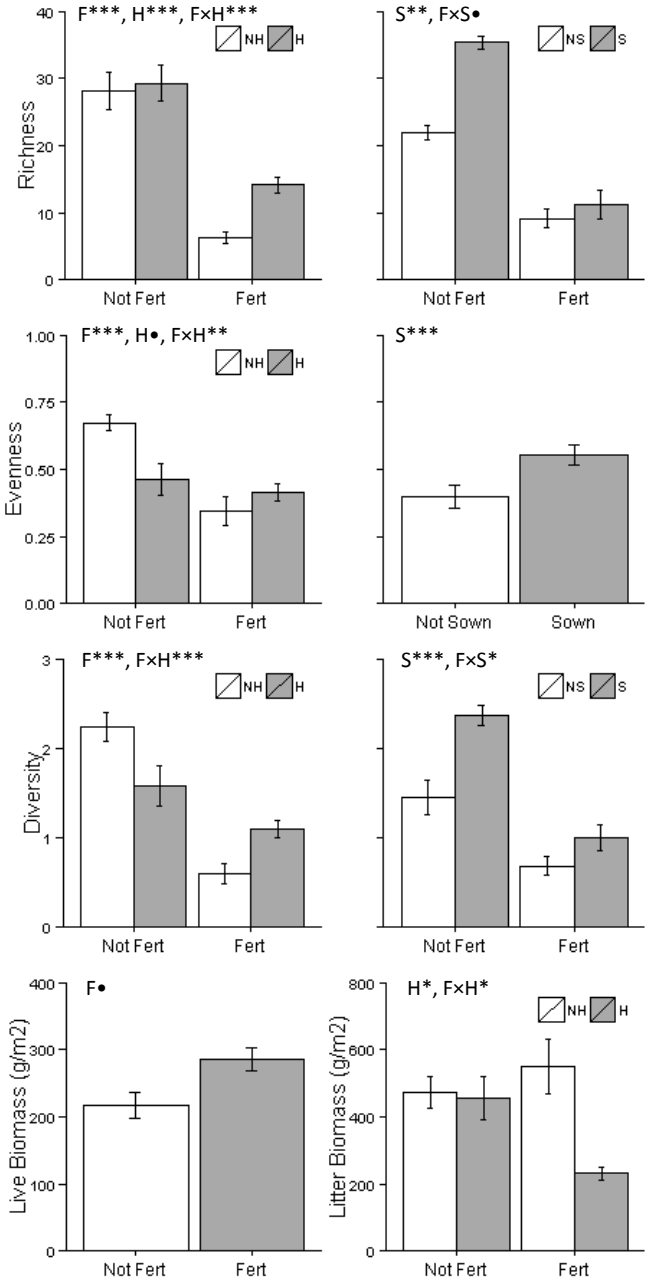


Figure 4. Plant species composition in response to fertilization, sowing, and haying (sowing effect: F = 4.910, p = 0.010; fertilization effect: F = 39.625, p = 0.001; haying effect: F = 3.7889, p = 0.007; fertilization × sowing interaction: F = 0.441, p = 0.011; fertilization × haying interaction: F = 25.8519, p = 0.001). Panels separated by haying treatment, and sowing levels (seeds added: +S; seed not added: -S) and fertilization levels (nitrogen added: +F; nitrogen not added: -F) described in legends.

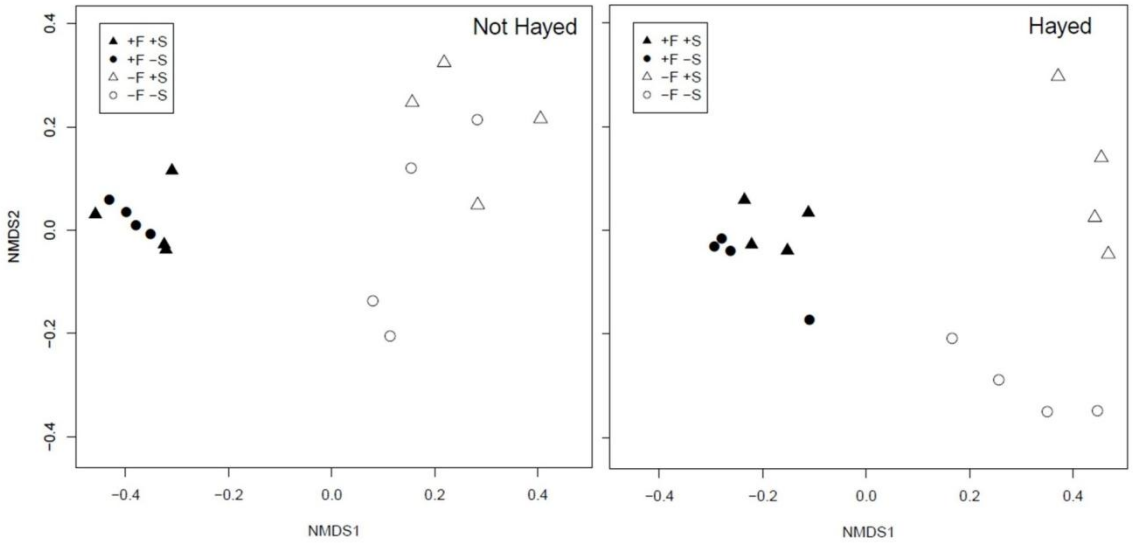


Figure 5. Responses of arthropod richness, evenness, diversity, and density to treatment effects. Response variables are shown on separate rows, and sampled communities are shown on separate columns (the entire arthropod community response is labeled as "whole"; aerial arthropods as "aerial"; vegetation-dwelling arthropods as "vegetation"; and substrate-dwelling arthropods as "substrate"). Significant effects and interactions are noted in upper left corner of each graph ("F" – fertilization effect; "H" – haying effect; "S" – sowing effect; "F×H" – fertilization by haying interaction; "S×H" – sowing by haying interaction; "S×H×F" – sowing by haying by fertilization interaction; "ns" – no significant effects) , and significance levels are included (*$p < 0.05$; **$p < 0.01$; ***$p < 0.01$). Legends are abbreviated as follows: "NH"/"H": not hayed/hayed; "NF"/"F": not fertilized/fertilized; "NS"/"S": not sown/sown. Note different y-axis scales and legends among panels.

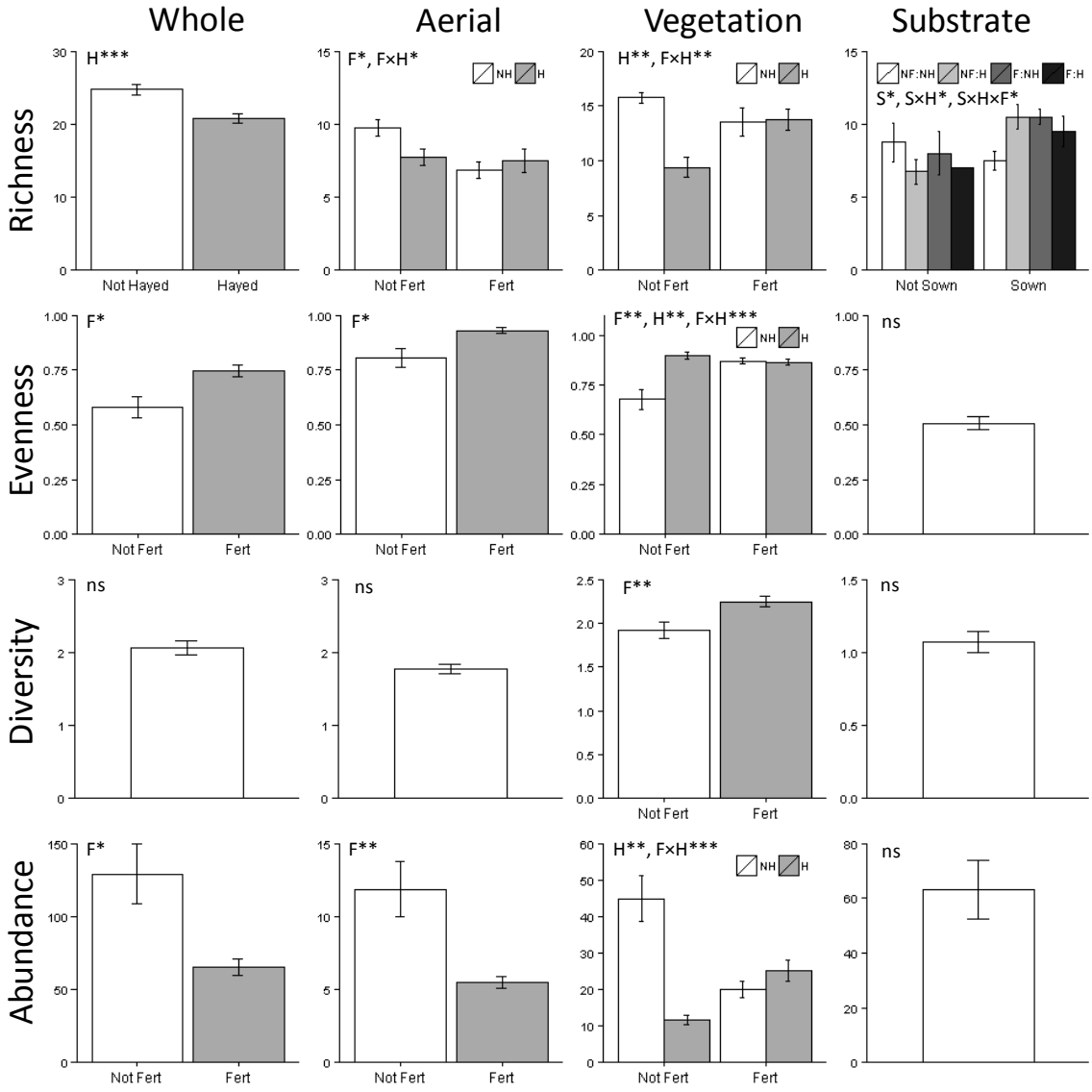


Figure 6. Arthropod OTU composition in response to fertilization and haying (fertilization effect: F = 9.4099, p = 0.0002; haying effect: F = 1.8677, p = 0.0239; fertilization × haying interaction: F = 5.4801, p = 0.0252). Levels of fertilization (nitrogen added: +F; nitrogen not added: -F) and haying (hayed: +H; not hayed: -H) described in legends.

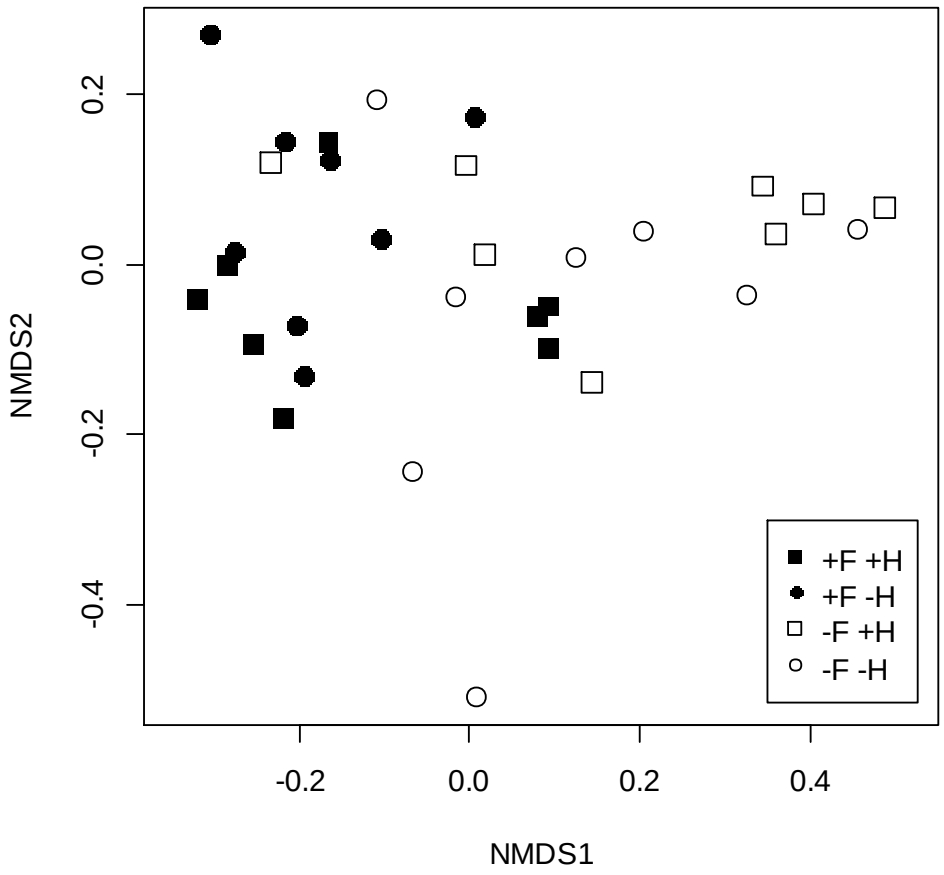
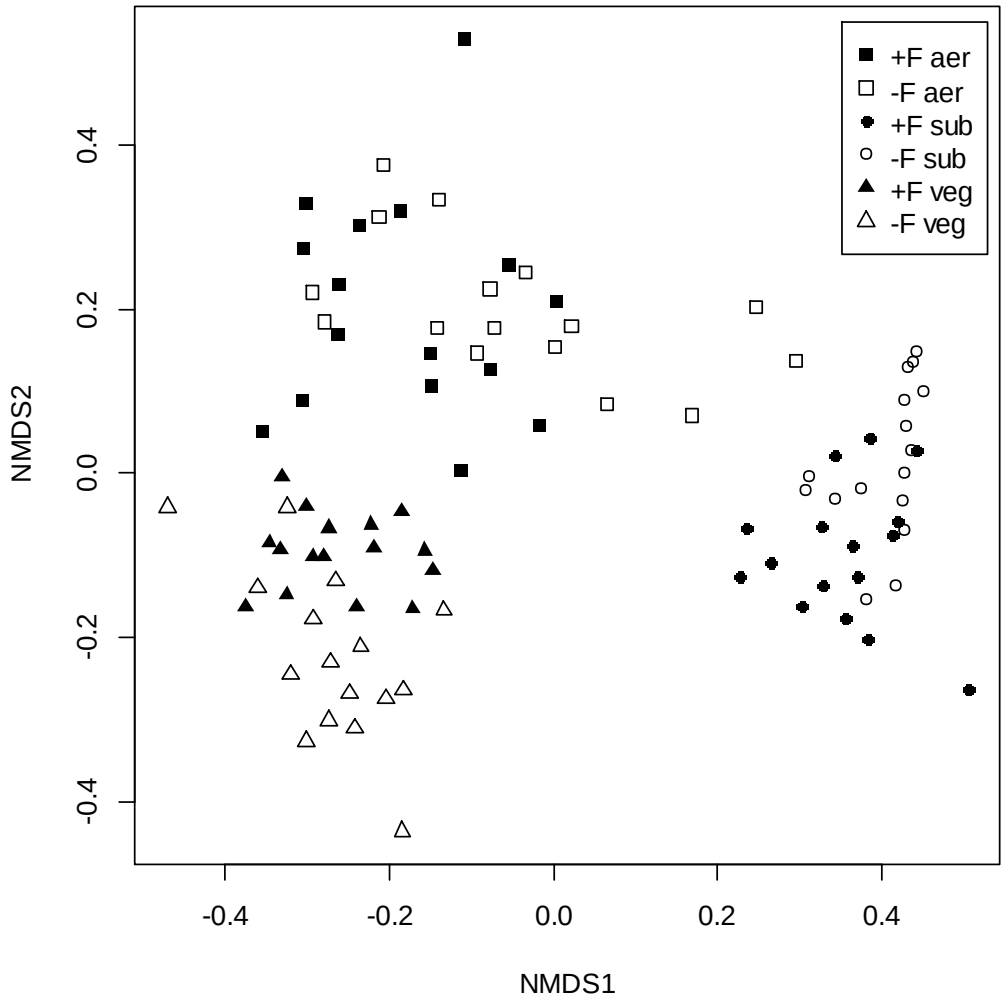


Figure 7. Arthropod OTU composition within each microhabitat in response to fertilization (microhabitat effect: $F = 5.566$, $p = 0.001$; fertilization × microhabitat interaction: $F = 50.270$, $p = 0.001$). Fertilization levels (nitrogen added: +F; nitrogen not added: -F) and microhabitat ("aer" – aerial arthropods; "sub" – substrate-dwelling arthropods; "veg" – vegetation-dwelling arthropods) described in legend.



APPENDIX:

Appendix A. List of plant species sown in experiment and each species' functional guild.

Species	Functional Guild*
Achillea millefolium	PNLF
Agastache nepetoides	PNLF
Amorpha canescens	PLF
Andropogon gerardii	C4-PG
Asclepias tuberosa	PNLF
Aster novae-angliae	PNLF
Astragalus canadensis	PLF
Bouteloua curtipendula	C4-PG
Cassia chamaecrista	AF
Dalea candida	PLF
Dalea purpurea	PLF
Desmanthus illinoensis	PLF
Echinacea pallida	PNLF
Elymus canadensis	C3-PG
Eragrostis trichodes	C4-PG
Eryngium yuccifolium	PNLF
Eupatorium altissimum	PNLF
Festuca ovina	C3-PG
Gentiana flavida	PNLF
Helianthus maximiliani	PNLF
Helianthus rigidus	PNLF
Heliopsis helianthoides	PNLF
Lespedeza capitata	PLF
Liatris pycnostachya	PNLF
Monarda fistulosa	PNLF
Oenothera missouriensis	PNLF
Panicum virgatum	C4-PG
Penstemon albidus	PNLF
Ratibida columnifera	PNLF
Ratibida pinnata	PNLF
Rudbeckia hirta	PNLF
Salvia azurea	PNLF
Schizachyrium scoparium	C4-PG
Silphium laciniatum	PNLF
Silphium perfoliatum	PNLF
Solidago rigida	PNLF
Sorghastrum nutans	C4-PG

Sporobolus cryptandrus	C4-PG
Teucrium canadense	PNLF
Verbena stricta	PNLF
Zizia aurea	PNLF
*Key to abbreviations: AF, annual forb; PLF, perennial leguminous forb; PNLF, perennial non-leguminous forb; C3-PG, perennial grass with a C_3 photosynthetic pathway; C4-PG, perennial grass with a C_4 photosynthetic pathway.	

GENERAL CONCLUSIONS:

Overall, the results of my thesis suggest that both local environmental factors (soil fertility, resource diversity, *etc*) and factors occurring at a larger regional scale (dispersal constraints and spatial processes) influence community diversity and structure of plants and consumers. The relative importance of local and regional processes varies over successional time (Chapter 1) and among nested guilds occupying different niche space (Chapter 2), suggesting that community responses are contingent on both temporal and spatial scales.

In Chapter 1, I test the relative importance of constraints due to seed/dispersal *versus* local soil fertility and competition on species diversity. I examine responses of community diversity over the first 11 years of secondary succession in a system subjected to a seed addition treatment (sowing of mid- to late-successional species) and fertilizer additions (4 levels of soil N; 2 levels of soil P). Overall, I find strong constraints of dispersal and seed availability on diversity through succession, in support of the species pool hypothesis (Eriksson, 1993; Zobel, 1997) and past demonstrations of seed limitation (Foster & Dickson, 2004; Foster et al., 2004; Foster & Tilman, 2003; Tilman, 1997). Yet, positive effects of seed addition diminished with time, suggesting that constraints to diversity shift from seed availability to local competition and microsite availability over the course of succession, in support of the successional shifting limitations hypothesis. Additionally, sowing level affected the strength and temporal manifestation of effects of nutrient additions on species richness, suggesting that dispersal constraints and seed availability of competition (late successional) species can mediate the effects of resource gradients on species coexistence. Nutrient additions generally reduced species richness, evenness, and diversity – consistent with past fertilization effects and the niche limitation hypothesis (Harpole & Tilman, 2007; Tilman, 1993; Wilson & Tilman, 2002). Positive

effects of seed addition on species richness, evenness, and diversity dampened under conditions of high soil N; suggesting constraints to diversity to shift from seed availability and dispersal abilities to local competition and microsite availability with increasing productivity as predicted by the productivity shifting limitations hypothesis, consistent with the productivity shifting limitations hypothesis.

My findings are consistent with past demonstrations recognizing the role of productivity in determining limits to diversity (Foster et al., 2004; Houseman & Gross, 2006; Myers & Harms, 2009; Stein et al., 2008), as well as well-recognized effects of species pools and niche limitation on diversity (see references above). Furthermore, this chapter provides novel insight into shifts in the dominant forces governing diversity through succession (*i.e.* shifting from seed to microsite limitation) and interactions between these gradients (*i.e.* seed availability of mid- to late-successional species mediates the temporal expression and strength of effects of soil fertility and local competition).

In Chapter 2, I test multiple hypotheses regarding the formation of consumer communities to determine the relative influence of 1) plant diversity, 2) plant abundance, 3) plant composition, 4) plant litter biomass, and 5) spatial processes on arthropod community structure. I sample arthropods inhabiting grassland plant communities undergoing long-term management regimes that differ in the resource attributes listed above (plant diversity, composition, *etc*) to test if arthropod responses track the aforementioned resource characteristics and/or track diversity-productivity relationships of plants (the dynamic equilibrium model (DEM): Huston 1979, 1994). Also, I conduct multiple regression and variance partitioning analyses to determine the relative influence of each factor on arthropod community structure.

Overall, I find support for resource diversity, plant litter density, plant species composition, and spatial processes in structuring whole arthropod communities. Additionally, by examining niche-specific responses of arthropod assemblages inhabiting different microhabitats, I find support for the DEM and effects of resource diversity, plant composition, and spatial processes in influencing community structure of specific assemblages.

My findings are consistent with past work demonstrating the roles of plant diversity (Haddad et al., 2009; Haddad et al., 2000; Siemann et al., 1998), plant species composition (Koricheva et al., 2000; Schaffers et al., 2008; Symstad et al., 2000), and plant litter density (Hansen, 2000; Wardle et al., 2006) in shaping consumer communities. Also, my findings emphasize the importance of spatial effects in community organization of multiple, distinct arthropod assemblages, suggesting that spatial processes and dispersal dynamics occurring among connected patches must be considered when identifying factors influencing community structure (Cottenie, 2005; Leibold et al., 2004). Consumer communities are highly complex and variable, yet this chapter highlights several factors that are likely to be highly influential in their assembly and development at multiple sampling scales (*i.e.* whole community and within nested microhabitats).

In summary, this thesis identifies several factors – operating at different spatial and temporal scales – that drive community structure and diversity of plant and arthropod communities. My results are relevant in the fields of restoration ecology and management of grassland ecosystems. Tallgrass prairies host highly diverse and productive organismal communities, yet their pronounced decline since the expansion of agriculture and anthropogenic development (Losey & Vaughan, 2006) makes this ecosystem of high interest to conservation.

By better understanding factors driving community assembly and diversity of this ecosystem, we can better inform its restoration and conservation.

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